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# THE INSECTS AND ARACHNIDS OF CANADA

# PART 13

## The Carrion Beetles of Canada and Alaska

## Coleoptera: Silphidae and Agyrtidae

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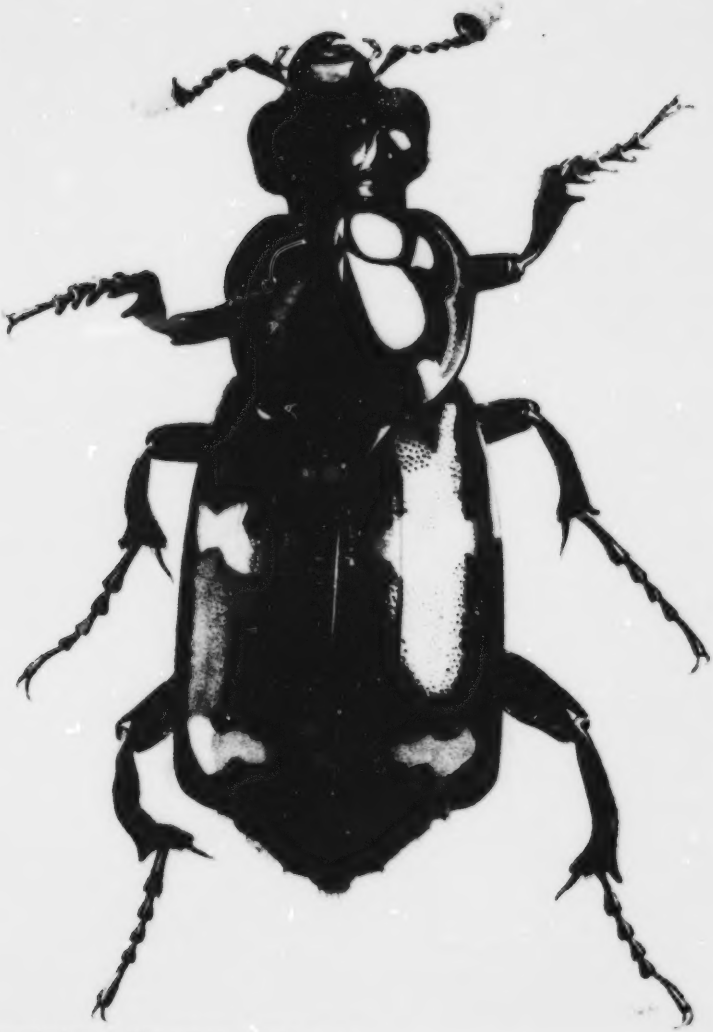

Frontispiece. *Nicrophorus sayi* Laporte.

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## Introduction

Many kinds of decaying organic materials are microhabitats commonly inhabited by a wide variety of beetles. In these materials, some beetles, such as the staphylinids, are predators. Others are scavengers, with both adults and larvae feeding directly upon the decaying material. Early entomologists considered most beetles sharing the scavenging habit of feeding on carrion to be members of a single family, the Silphidae (*sensu lato*), but subsequent studies have indicated that this is an unnatural assemblage. The group has now been split into smaller units and each unit has been given separate family status.

Arnett's (1968) concept of the Silphidae is used by many entomologists and includes the tribes Lyrosomini, Agyrtini, Silphini, and Nicrophorini. Recently, the Lyrosomini and Agyrtini have been transferred out of the Silphidae and given separate family status as the Agyrtidae (Lawrence 1982; Lawrence and Newton 1982). The Silphidae, as treated here, currently only contains the Silphinae and Nicrophorinae. Because silphids and agyrtids have traditionally been considered as a single family in all existing keys to beetle families and because this is the classification familiar to most people, we have treated both families in this book. We do, however, regard the two as distinct families and present a key to permit proper placement of adults. Detailed familial diagnoses are not presented but can be found in Lawrence (1982).

The aim of this book is threefold: (*1*) to provide a means of identifying adults of the various species of the families Silphidae and Agyrtidae and larvae of the various species of silphids known to occur in Canada and Alaska; (*2*) to review available biological information; and (*3*) to document the distributions of all these species in North America.

## Methods

All species known to occur in Canada and Alaska are considered here. Illustrated keys are given for the identification of adults and known larvae of all genera and species of North American silphids, north of Mexico, and of adults of all genera and species of North American agyrtids, north of Mexico. However, only those species occurring in Canada or Alaska are treated in further detail. The species treatments include the following information: North American (used hereafter to mean north of Mexico) synonymy, a brief diagnosis of the adult, a brief diagnosis of the larva (if known), a brief statement of the species distribution, a detailed distribution map showing localities where specimens of each species have been collected in Canada and Alaska, a map showing the approximate distribution of each species in the United States, a brief summary of the natural history of the species, fossil records of the species in North America, and notes on geographic variation of adults.

Keys to larvae and larval diagnoses are based on third instar larvae, though available material indicates that the keys will also work for earlier instars. Detailed larval descriptions, if available, are cited following larval diagnoses. We should state here that the keys to species of larval silphids may prove unreliable when larvae of other species are described. For now, attention should be given to the larval diagnoses and species distributions when using these keys, because this information may enable the user to recognize undescribed larvae. The key to the genera of larval silphids is based on examination of Palearctic as well as Nearctic taxa.

Complete citations of synonymy can be found in Portevin (1926), Hatch (1928), Miller and Peck (1979), Madge (1980), and Peck and Miller (1982). Madge (1980) lists type species for all genera of silphids and agyrtids. Detailed lists of specimen locality and label data are not presented, but this information is available from the authors.

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## Key to families of adults

1. Size small, 9–13 mm long; each elytron with 9 or 10 striae, covering entire abdomen ..... **Agyrtidae** (p. 73)
   Size large, 10–35 mm long; each elytron tricostate or else lacking costae entirely, in some species truncate and exposing 3 or 4 abdominal segments ..... **Silphidae** (p. 11)

## Tableau de détermination des familles (adultes)

1. Taille petite, de 9 à 13 mm de long; élytres avec 9 ou 10 stries chacun, recouvrant entièrement l'abdomen ..... **Agyrtidae** (p. 73)
   Taille grande, de 10 à 35 mm de long; élytres avec 3 costae chacun, ou sans costa, tronqués chez certaines espèces et exposant 3 ou 4 segments abdominaux ..... **Silphidae** (p. 11)

## Silphidae

Members of the family Silphidae are large beetles, 10–35 mm long, frequently found associated with decaying organic material. They are most commonly encountered at vertebrate carcasses and hence have the common name of carrion beetles. The habit of adults of some family members of interring small vertebrate carcasses has also led to the use of the common names of sexton beetles and burying beetles.

The North American silphids were revised by LeConte (1853) and subsequently by Horn (1880). All species were placed into two genera, *Nicrophorus* and *Silpha*. Revision of the world fauna by Portevin (1926) divided the genus *Silpha* into numerous genera. This revision incorporated genera proposed by Leach (1815) and also erected many new ones. This generic system has been refined and is in widespread use in Europe and Asia, but the concepts have not been applied consistently or correctly to the North American fauna (see Arnett 1944; Hatch 1927*a*, 1928, 1957). Only recently (Peck in press; Miller and Peck 1979) have generic concepts been applied to the Nearctic species in a way consistent with that for the Palearctic species.

There are 30 species in 8 genera in North America, north of Mexico, 25 of which have distributions entirely or partly in Canada and Alaska.

## Natural history

Most Silphidae are necrophagous as adults and as larvae. Members of some Palearctic genera are snail or caterpillar predators (*Dendroxena* Motschulsky and some *Silpha* Linnaeus *sensu stricto*), whereas some, if not all, members of species of *Aclypea* are phytophagous. Adults of many species are also found at fungi, dung, or decaying vegetable material. Although all larvae of the necrophagous species appear to feed exclusively on decaying animal flesh, adults of some of these species not only feed on carrion but also on other insects, especially fly larvae (Balduf 1935; Clark 1895; Steele 1927), which they encounter at carcasses.

Studies on a few species have shown that olfaction is of primary importance in finding food (Dethier 1947; Abbott 1927*a*, 1927*b*), with the sensilla coelosphaerica of the terminal antennal segments being the principal olfactory structures involved (Boeckh 1962; Ernst 1969, 1972; Waldow 1973). These sensilla are sensitive to hydrogen sulfide and some cyclic carbon compounds (Waldow 1973), which are released as a carcass decays. The role of wind in the orientation behavior of adult beetles to food sources has also been examined (Shubeck 1968; Petruska 1975), but the results are inconclusive.

**Economic importance.** Adults of some European species carry various parasitic nematodes and cestodes, although none of these are known to infect man or domestic animals (Prokopic and Bily 1975). Studies to investigate the possibility that silphids could carry and disseminate rabies virus and anthrax bacilli have also been made. These studies showed that rabies virus is inactivated in the gut of *Nicrophorus* (Sidor 1970), but that anthrax bacilli could be disseminated by silphids (Osinskii 1940). Silphids are also important components of ecosystems, because they assist in the promotion of nutrient recycling. They are also significant in that they remove potential breeding sites for many species of noxious flies.

Species of *Aclypea* are phytophagous and can be serious pests of several crop plants.

**Life cycles.** There are two subfamilies in the Silphidae, the Silphinae and the Nicrophorinae, and members of each one have developed radically different methods of carrion resource use.

Of the two life cycle patterns, that of the genus *Nicrophorus* in the subfamily Nicrophorinae is the more complex. Its life cycle, first elucidated in detail by Pukowski (1933), can be summarized as follows: Adult beetles, upon finding a small dead animal such as a mouse or vole, will crawl over and under the carcass. These activities have been interpreted as means by which the insects assess the suitability of the carcass for burial. The carcass, if suitable, can be buried where it lies, or it may be moved to a place where the substrate is more suitable for burial. The method by which the beetles move and bury carcasses has been described and illustrated by Milne and Milne (1976). Burial results from the beetles burrowing into the soil on one side of the carcass, continuing to burrow under it, and then pushing the soil out the other side as they emerge. This behavior continues until the carcass sinks into the cavity or is pulled in by the beetles from below. Subsequent movements by the beetles around the carcass, after it has been buried, result in the formation of a cryptlike chamber with the carcass lying in the center.

Usually only a pair of adult beetles is associated with a carcass. However, more than one pair or even more than one species may be initially present. When more than a single pair is present, fighting ensues until only one pair remains to use the resource for reproductive purposes. This fighting usually takes place after the food source has been buried. The victorious pair then prepares the carcass by molding it into a sphere and stripping it of fur or hair. The female then excavates a passage leading off in a lateral direction from the chamber, where, within 48 hours (Wilson and Knollenberg 1984) she lays up to 30 eggs in the walls of the passage. After oviposition the male, his reproductive investment ensured, always leaves the chamber.

After the larvae hatch, they move to the carrion food source. The female then chews a hole in the exterior surface of the carrion ball and exposes the inner contents. Larvae crawl into this hole but do not yet feed. Then the female regurgitates a liquid, which is imbibed by the larvae as their mouth-

parts contact hers. This continues for about 5 or 6 hours. Then the larvae begin to feed on their own. Feeding of larvae by adult females also takes place after the first and second molts, but this feeding does not appear to be obligatory, since the larvae will mature even if the female is removed.

There are three larval instars; the first lasts about 12 hours, the second about 24 hours, and the third from 5 to 15 days, depending on the species and conditions. Upon completing their development, larvae crawl into the surrounding soil to pupate. The pupal stage lasts from 13 to 15 days, and it is at this time that the female leaves the chamber.

Phoretic mites are invariably present on *Nicrophorus* adults and may be involved in a symbiotic relationship with the beetles. These mites feed on any fly eggs that may be in the surrounding soil or on the carcass and which would otherwise hatch into maggots, competing for the carrion (Springett 1968). In turn, the mites receive transportation to and from food sources that would otherwise be inaccessible to them, because carcasses are randomly distributed in place and time, and are a highly unpredictable resource.

Four families of mites occur on the beetles: Parasitidae, Anoetidae, Uropodidae, and Macrochelidae. *Poecilochirus* mites (Parasitidae) form the largest and most active group of mites on the adult beetles, and is the group implicated by Springett (1968) as being involved in a symbiotic relationship with the beetles. The relationships and possible roles of the other mites have not yet been examined in detail, although D. S. Wilson of Michigan State University is studying this aspect of silphid natural history (Wilson 1983).

It therefore appears that *Nicrophorus* beetles avoid competition with flies and other scavengers by burying the larval food resource, developing rapidly, and having an assemblage of commensals which render the food unsuitable for consumption by other potential competitors.

By reason of size, only small carcasses can be completely buried for reproductive purposes. *Nicrophorus* beetles thus do not compete with the Silphinae, which use large carcasses for food. Occasionally, however, adult species of *Nicrophorus* are found on large carcasses where they eat either carrion or fly larvae to meet their own nutritional requirements (Wilson and Knollenberg 1984). *Nicrophorus* adults may also be found feeding at dung or decaying fungi.

In contrast to *Nicrophorus*, the life cycle of genera of the Silphinae is less complex and can be summarized as follows: Adult beetles, upon finding a dead animal, will mate. The females subsequently oviposit in soil around the carcass. Within 2–7 days the larvae hatch, move to the carcass, and begin to feed. There are three larval instars, the first usually lasting 3–7 days and the second and third each usually lasting 3–10 days. Pupation takes place in the soil and appears to last 14–21 days. Unlike *Nicrophorus* species, these beetles appear to avoid competition with numerous fly larvae at a carcass

by waiting until the fly larvae have finished feeding. This happens because the beetle eggs hatch when the fly larvae are moving from the carcass to the soil in order to pupate. This is approximately 5 days after oviposition by both taxa. The silphine larvae then feed on the remains of the carcass (Dorsey 1940; Johnson 1974). Larval development is much slower than in *Nicrophorus*. Silphine adults are also occasionally found at dung and garbage, but it is unusual for them to breed there.

In the Silphinae there are no known larval/parental interactions, such as those which occur in *Nicrophorus*. Phoretic mites are seldom found on adult Silphinae. This would be expected, because members of the Silphinae would not benefit from the presence of such mites.

Silphids appear to divide available food resources through differential use of habitats and by having different seasonal patterns of development. Studies on this aspect of the natural history of North American species are few. Anderson (1982*a*) presented a detailed analysis of resource partitioning in eastern North American *Nicrophorus* and Silphinae. The natural history of Palearctic silphids has been studied in greater detail than that of Nearctic species, but regional ecological studies are sorely lacking.

**Defense.** Adult individuals of *Nicrophorus* possess a pair of stridulatory files on the fifth abdominal tergite (Fig. 24). The structure of the files is apparently species specific (Schumacher 1973). These files are rubbed on the apex of each elytron and produce a scraping sound, which is used in defense. This scraping sound is also possibly used in communication between individuals (Schumacher 1973; Niemitz 1972). When disturbed, the beetles often stridulate, sounding like a bee, and will frequently then go into a state of thanatosis. On occasion, they move the apical segments of the abdomen in much the same way that a bee does when everting a stinger (Lane and Rothschild 1965). They can also emit a foul-smelling fluid from the anus, which is presumably also foul tasting or possibly even toxic to any organism that might ingest it. The contrasting orange and black color pattern of most *Nicrophorus* adults (frontispiece) may also play a defensive role by being aposematic and it could deter potential predators, as has been noted by Jones (1932). Diffraction gratings in both Silphinae and *Nicrophorus* produce an irridescent color pattern that may also deter or confuse predators (Hinton 1969).

Among species of Silphinae, Eisner and Meinwald (1982) have demonstrated the unacceptability of *Necrodes surinamensis* to bird predators. They have also demonstrated that adult beetles spray a foul-smelling, acidic fluid, which is secreted by a rectal gland, from the anus. This fluid can be directed at potential predators by the beetle aiming its abdominal apex at the intruder.

## Methods of collecting and rearing specimens

Because of their habits, silphid adults and larvae are quite easy to collect. Simply by overturning dead animals (those killed on the road are the most frequently encountered), one will usually find numerous specimens. This method, however, is dependent on the collector finding carrion and does not always ensure a high species diversity in the catch, because many species of *Nicrophorus* are not commonly found at large carcasses. A much better method is to use pitfall traps, baited with carrion (Newton and Peck 1975). We recommend using fish, chicken legs, or chicken wings for bait, because these items are readily available, are relatively inexpensive, and have been used extensively by us with good results.

Many beetles, both silphids and others, are attracted rapidly and in large numbers to the carrion bait if it is especially ripe. In order to ensure maximum attractiveness in the bait, ripen it for 1–2 days in a closed container or glass jar placed in a warm, well-ventilated place, such as a sunny backyard. Then select a suitable site for trapping and dig a hole into the ground. Place a container (we use plastic ice-cream containers or large tins) into the hole so that the edge of the container is flush with the soil surface, and pack the soil around the edge of the container. This is done to eliminate any obstacle that might impede the movement of the beetles. Next, put the ripe carrion (use about two chicken wings or one chicken leg per trap) onto a 20-$cm^2$ piece of loosely woven cloth (cheesecloth is best). Lift four corners of the cloth so that the bait is suspended in the bag which is formed. Tightly wind these corners together with fine wire, making sure that the carrion is firmly suspended and will not fall out. Then wind the free end of the wire around a stick or, preferably, the mesh of a piece of coarse screen (chicken wire is suitable) that is large enough to cover the opening of the trap. Openings in the screen should be large enough to let beetles into the trap. Next, pour a preservative, preferably a saturated salt solution or ethylene glycol (automobile radiator antifreeze), into the trap to a depth of about 5 cm. Place the wire mesh, from which the bait is suspended, over the trap, making sure that the bait does not touch the edges of the trap or the preservative. These situations lead to inefficient traps and very messy catches.

If large mammals such as raccoons or skunks are present in the area it is best to place three or four large rocks on the edges of the chicken wire. Cover the rocks with a piece of plywood (or something similar) to keep out rain, and put another rock on top of the plywood to keep it from being removed by animals or by wind. This procedure will usually keep scavengers from stealing the bait and ensure that the preservative is not diluted. For best effectiveness, traps should be cleared at intervals of 3–5 days. Bait can be used for as long as 2–3 weeks in cool weather, although attractiveness decreases with extended use.

It is important to trap in different habitats, because some species are associated with particular environmental conditions. We recommend placement of traps in marshes or bogs and in meadows or grasslands, as well as in forested areas.

The phytophagous species in the genus *Aclypea* are best collected by searching the host plants. If this method fails, place unbaited pitfall traps, into which the beetles may fall, in areas where the host plants are common. These unbaited traps can then be left and, like the baited traps, checked at regular intervals. For unbaited traps, shallow pans with larger surface areas are recommended. During their movements, more insects are likely to fall into these larger surface area traps.

Although unpleasant to some individuals, rearing members of the genus *Nicrophorus* can be very interesting, and is usually the only way of acquiring larvae. Their adult habits, pair cooperation, and family history are among the most fascinating in the insect world and have attracted the interests of such noted naturalists as J. H. Fabre.

Members of *Nicrophorus* can be reared by placing a male and a female into a container, which has been filled to a depth of 15–20 cm with moist sandy soil. Then place a dead mouse, or other similarly sized piece of carrion, on the soil surface and cover the container. Within a few hours, the beetles will begin to bury the carrion. This task can be observed by removing the lid, although such an action will cause individuals of most species to scurry under the soil. Using a red light or even a flashlight at night will help avoid this problem. After the mouse has been buried there is nothing much to observe unless, of course, a glass viewing chamber is assembled. We have never attempted this, but such a chamber has been used by other workers. Soon after burial, the male will attempt to leave the container and can be removed at this time. Excavation of the carrion, about 2 weeks later, will usually yield numerous larvae. The female will still be present and will attempt to defend them. She may also stridulate in an attempt to scare you away.

For rearing purposes, it is important that specimens be collected early in spring. Most species of *Nicrophorus* breed at this time and attempts by us to rear them later in the year have not met with success. Some species, however, may only be reared during the latter part of summer and early fall. Further details on seasonalities are given later in the text.

Because of their habits, extra caution regarding hygiene should be exercised when working with silphids.

## Adult anatomy

A general anatomical characterization of the family is presented later in the text. In order to facilitate the understanding of structural terms and use of the keys contained in this handbook, a brief illustrated discussion of

silphid anatomy is provided. This discussion is by no means comprehensive and is only intended to emphasize and aid in the recognition of the conditions of taxonomically important characters.

**Antennae:** Antennal structure is characteristic for each of the two subfamilies of silphids. The Silphinae have antennae that are gradually clavate from segments 7–11 (Fig. 20). In these, the second segment is large and easily seen. In the genus *Nicrophorus*, the antennae are capitate; the apical four segments form a loose club (Fig. 21). The second segment is small and difficult to see. Within *Nicrophorus*, the color of the apical three segments of the antennae is an important character for separating certain species. Shape and vestiture of some segments of the club is also a valuable character.

**Clypeus:** In silphines, the clypeus and the labrum are fused; thus no epistomal suture is present (Fig. 2). Members of *Nicrophorus* possess the epistomal suture, but the clypeus is modified and a large membranous area is present (Fig. 1).

**Labrum:** A deeply emarginate labrum is important in recognizing members of the genus *Aclypea* (Fig. 3).

**Eyes:** Eye size is a character that is often used to separate silphine genera (Fig. 4). Of greater importance as a taxonomic character, however, is the presence or absence of a row of long erect hairs just behind the eyes. These hairs are present in the genera *Oiceoptoma, Heterosilpha*, and *Necrophila* (Fig. 2).

**Pronotum:** In the Silphinae, the pronotum is broad, usually wider than long, and broadly explanate (Figs. 15, 16). In *Nicrophorus*, the pronotum is narrower and at most is only narrowly explanate (Figs. 39–43). In most species the pronotum is entirely black, but in some silphines it is brightly colored. In *Nicrophorus*, only one species, *N. americanus*, has a colored pronotum. The pronotum of *N. tomentosus* is covered with a dense, yellow pubescence.

Shape of the pronotum is also important. In the Silphinae, most species possess a pronotum that has its greatest width behind the middle (Fig. 16). However, the genus *Necrodes* has an orbicular pronotum that has its greatest width at the middle (Fig. 15). Certain species groups of *Nicrophorus* can also be characterized by pronotal shape. These shapes are as follows: cordate (Figs. 42, 43), subquadrate (Fig. 41), quadrate (Fig. 40), and orbicular (Fig. 39). It is often difficult to distinguish subquadrate from quadrate pronota.

Associated with the pronotum is the postcoxal lobe, which can easily be seen in a lateral view of the thorax (Figs. 17–19). Its shape is sometimes used in the taxonomy of silphines.

**Elytron:** Silphids usually possess three ridges, or costae, on each elytron (Figs. 8, 12, 13), although in some the costae are either vaguely defined or

lacking (Figs. 6, 10). The latter is the situation with all species of *Nicrophorus*. The elytral apices are prolonged in silphines, whereas in *Nicrophorus* they are truncate, often resulting in three or four abdominal segments being exposed (frontispiece). Some silphines have tubercles (Fig. 7) or reticulate sculpturing (Figs. 11, 14) on the elytral surface. Such sculpturing is not present in *Nicrophorus*.

In most silphids the elytra are either black or brown, but in *Nicrophorus* they are often colored with bright red or orange markings (frontispiece). The position and extent of these markings are valuable taxonomic characters for aiding in the separation of species of *Nicrophorus* (Figs. 45–72), but they should be used in conjunction with other characters. Color of the elytral epipleuron is also an important taxonomic character for recognizing members of a few species of *Nicrophorus*, as is the length of the epipleural ridge (Figs. 45, 46).

**Metathorax:** Important taxonomic structures are found on the metathorax. Of great importance for the recognition of species groups in *Nicrophorus* is the presence or absence of hairs on the metepimeron (Fig. 5). The density and color of these hairs and the color of metathoracic vestiture (Fig. 5) are also important. Some species of *Nicrophorus* also possess a bald spot just behind each mesocoxa (Fig. 5).

**Legs:** Leg characters, which are important in silphid taxonomy, are as follows. The length of the hairs on the anterior faces of the bases of the procoxae is important for separating some species of *Nicrophorus*. The degree of curvature of the hind tibiae also provides for easy recognition of certain *Nicrophorus* species.

**Genitalia:** Few references are made to genitalia in this book. This is not to say that they are not useful taxonomic tools; they are. However, it is not necessary that they be used to provide reliable and accurate species identifications. As with many other characters not discussed here, their ultimate value probably lies in aiding an understanding of evolutionary relationships among silphid taxa.

## Larval anatomy

As with adults, a familial diagnosis is presented elsewhere in the text. This section serves only to emphasize and aid in the recognition of taxonomically important character states.

**Antennae:** The antennae of larval silphids are three-segmented, with the second segment bearing a sensory area near the apex. This sensory area can be composed of a single large cone surrounded by smaller cones, or from one to many plates. Members of *Nicrophorus* and some silphine genera possess the cones (Fig. 75), whereas members of *Aclypea, Heterosilpha*, and

*Necrophila* possess plates (Figs. 76, 77). Members of *Aclypea* possess a single large plate (Fig. 77).

**Labium:** In members of most species of *Nicrophorus*, the labial palpi have the first segment sclerotized ventrally and the palpi widely separated (Fig. 97). In *N. defodiens, N. vespilloides*, and *N. sayi* the palpi have the first segment unsclerotized ventrally and are close together (Fig. 98).

**Ocelli:** In members of the Silphinae, there are six pigmented ocelli on each side of the head. In members of *Nicrophorus*, this number is reduced to a single unpigmented ocellus on each side of the head.

**Urogomphi:** In members of the Silphinae, the length and number of segments of the urogomphi are very important for separating genera. In *Necrodes, Oxelytrum*, and *Thanatophilus* the urogomphi are distinctly longer than the 10th abdominal segment (Figs. 79, 80). In the other genera they are equal to or only slightly longer than the length of the 10th abdominal segment (Figs. 78, 81–83). They are the longest in members of *Necrodes* and *Oxelytrum*. Members of *Aclypea* and *Heterosilpha* possess one-segmented urogomphi (Figs. 78, 81), whereas in all other silphid larvae they are two-segmented.

In members of *Nicrophorus*, the urogomphi of most species each have a suture at the base where they join the tergite of the ninth abdominal segment. These sutures are lacking in members of some species and in others are incomplete at the middle.

**Thoracic and abdominal sclerotization:** Members of *Nicrophorus* are easily recognized by their reduced sclerotization. They are almost wholly white, soft, and "grublike" in general appearance. They are best characterized by the presence of small, quadrispinose abdominal tergites (Fig. 89). On these tergites, the length of the middorsal spines relative to the lateral spines is important in *Nicrophorus* larval taxonomy. The extent of the ventral sclerotization of the ninth and 10th abdominal segments is also important for separating larvae of *Nicrophorus*. The ventral sclerotization of the 10th abdominal segment can be complete (Figs. 90, 92) or incomplete (Fig. 91) at the base. In *N. investigator* and *N. nigrita*, the apex of the 10th abdominal segment is sclerotized, forming a Y-shaped pattern (Fig. 92). This pattern is absent in all other Nearctic species of *Nicrophorus*.

Members of the Silphinae are more extensively sclerotized, with sternites and tergites large and well-defined. The tergites are laterally produced to varying degrees and are widest in members of *Oiceoptoma* (Figs. 86, 87). The abdominal tergites usually have the posterior angles pointed in Silphinae (Figs. 84–88). Sternites are large, covering most of the venter of each segment. The second abdominal sternite is either entire (Fig. 74) or broken into three separate sclerites (Fig. 73); this character is important for separating various genera.

**Color:** In silphine larvae, dorsal coloration is especially important for recognizing genera, and species within particular genera. Color ranges from uniformly dark brown to black in members of *Heterosilpha, Aclypea*, and *Necrophila*, to predominantly reddish brown with various amounts of whitish present in members of *Oiceoptoma, Necrodes*, and *Oxelytrum* (Figs. 84–87). Within *Oiceoptoma* and *Thanatophilus*, color patterns serve to distinguish members of the species for which larvae are known.

The midline of many silphine larvae is pale, but this is due to features associated with molting and varies from individual to individual. It is therefore an unreliable character and should not be used to distinguish taxa of Silphidae.

## Family Silphidae

Adult members of the Silphidae can easily be recognized by their large size; possession of clavate or capitate 11-segmented antennae (Figs. 20, 21); prominent fore coxae; elytra often being truncate (frontispiece), tricostate (Fig. 12), or lacking costae (Fig. 10), generally blackish, often with orange or red markings.

Larvae are characterized by the lack of a molar part on the mandibles; maxilla with mala fused to stipes, divided at apex into galeal and lacinial lobes, the galeal lobe bearing a large apical brush of setae, the lacinial lobe spinose only on the lateral margins; labium with ligula bilobed; and abdomen bearing well-developed, usually articulated one- or two-segmented urogomphi (Böving and Craighead 1930; Crowson 1967; Kasule 1966; Anderson 1982*b*).

Two subfamilies, the Silphinae and the Nicrophorinae, are recognized.

The family historically has included many other taxa currently not regarded as silphids. Most notable among these taxa are members of the Agyrtidae, which although still considered by some authors as silphids are now interpreted as not being closely related to the latter. Unpublished revisionary studies of A. F. Newton, Jr., at Harvard University indicate agyrtids are closely related to the Leiodidae and not to the Silphidae (Lawrence and Newton 1982).

### Key to subfamilies and genera of adult Silphidae of North America

1. Elytra truncate, exposing 3 or 4 abdominal tergites, usually with red or orange maculations (frontispiece). Fifth abdominal segment with stridulatory files on dorsum (Fig. 24). Epistomal suture present (Fig. 1). Second antennal segment small, indistinct, hidden in tip of first antennal segment (Fig. 21) ..... **Nicrophorinae** ..... ..... ***Nicrophorus* Fabricius** (p. 47)

Elytra usually not truncate, at most exposing 1 or 2 abdominal tergites. Fifth abdominal segment lacking stridulatory files. Epistomal suture absent (Fig. 2). Second antennal segment large, not hidden in tip of first antennal segment (Fig. 20) ..... **Silphinae** ..... 2

2(1). Pronotum with disc black, margins yellow ..... 3
Pronotum entirely black, or, with disc black, margins orange red ..... 4

3(2). Elytra with intervals smooth, and with apices drawn out to needlelike points (Fig. 13) ..... ***Oxelytrum* Gistel***
Elytra with intervals with reticulate sculpturing, and with apices not drawn out to needlelike points (Fig. 11) ..... ***Necrophila* Kirby & Spence** (p. 32)

4(2). Eyes large (Fig. 4). Pronotal postcoxal lobe short, rounded (Fig. 17); pronotum orbicular, widest toward middle (Fig. 15). Males with hind femora greatly expanded ..... ***Necrodes* Leach** (p. 30)
Eyes small. Pronotal postcoxal lobe well-developed; pronotum not orbicular, widest toward base (Fig. 16). Males with hind femora not expanded ..... 5

5(4). Head with short row of long erect hairs behind eyes (Fig. 2) ..... 6
Head without row of long erect hairs behind eyes (Fig. 3) ..... 7

6(5). Elytral shoulders with tooth (Fig. 22). Metafemur lacking carinae on inner face. Elytra without reticulate sculpturing ... ***Oiceoptoma* Leach** (p. 34)
Elytral shoulders rounded, not toothed. Metafemur with 2 carinae on inner face. Elytra with intervals with reticulate sculpturing (Fig. 14) ..... ***Heterosilpha* Portevin** (p. 28)

7(5). Labrum deeply emarginate (Fig. 3). Mesocoxae narrowly separated ..... ***Aclypea* Reitter** (p. 24)
Labrum shallowly emarginate. Mesocoxae widely separated ..... ***Thanatophilus* Leach** (p. 40)

*One species of this predominantly Neotropical genus, *Oxelytrum discicolle* Brulle, has a distribution extending into extreme southern Texas.

## Tableau de détermination des sous-familles et genres de Silphidae (adultes) d'Amérique du Nord

1. Élytres tronqués, exposant 3 ou 4 segments abdominaux, ordinairement avec des taches rouges ou orangées (frontispice). Cinquième segment abdominal avec un organe de stridulation (fig. 24). Suture épistomale présente (fig. 1). Deuxième article antennaire petit, indistinct, caché dans l'extrémité du premier article (fig. 21) ..... **Nicrophorinae** ..... ***Nicrophorus* Fabricius** (p. 47)
Élytres généralement non tronqués, exposant au plus 1 ou 2 segments abdominaux. Cinquième segment abdominal sans organe de stridulation. Suture épistomale absente (fig. 2). Deuxième article antennaire grand, non caché dans l'extrémité du premier article (fig. 20) ..... **Silphinae** ..... 2

2(1). Pronotum avec le disque noir et les marges jaunes ..... 3
Pronotum entièrement noir, ou avec le disque noir et les marges orangé rouge ..... 4

3(2). Élytre avec les interstries lisses, et l'apex prolongé en une fine pointe (fig. 13) ..... ***Oxelytrum*** **Gistel***

Élytre avec les interstries montrant une sculpture réticulée et l'apex non prolongé en une fine pointe (fig. 11) ..... ***Necrophila*** **Kirby & Spence** (p. 32)

4(2). Yeux grands (fig. 4). Lobe postcoxal du pronotum court et arrondi (fig. 17); pronotum arrondi et plat, sa largeur maximale vers le milieu (fig. 15). Fémurs postérieurs des mâles souvent très dilatés ..... ***Necrodes*** **Leach** (p. 30)

Yeux petits. Lobe postcoxal du pronotum bien développé; pronotum non arrondi et plat, sa largeur maximale vers la base (fig. 16). Fémurs postérieurs des mâles non dilatés ..... 5

5(4). Tête avec une courte rangée de longues soies droites en arrière des yeux (fig. 2) ..... 6

Tête sans rangée de longues soies droites en arrière des yeux (fig. 3) .. 7

6(5). Épaule de l'élytre avec une dent (fig. 22). Fémurs postérieurs sans carène sur la face interne. Élytre sans sculpture réticulée ..... ***Oiceoptoma*** **Leach** (p. 34)

Épaule de l'élytre arrondie, non dentée. Fémurs postérieurs avec 2 carènes sur la face interne. Élytre avec une sculpture réticulée par intervalles (fig. 14) ..... ***Heterosilpha*** **Portevin** (p. 28)

7(5). Labre très échancré (fig. 3). Coxae médianes peu séparées ..... ***Aclypea*** **Reitter** (p. 24)

Labre légèrement échancré. Coxae médianes très séparées ..... ***Thanatophilus*** **Leach** (p. 40)

*La répartition géographique d'une espèce de ce genre surtout Néotropical, *Oxelytrum discicolle* Brullé, atteint l'extrême-sud du Texas.

## Key to subfamilies and genera of larval Silphidae of North America

1. Tergites small, those on the abdomen quadrispinose (Fig. 89); ventral surface whitish and soft, lacking large sternites. Head with 1 unpigmented ocellus on each side ..... **Nicrophorinae** ..... ***Nicrophorus*** **Fabricius** (p. 47)

Tergites large, laterally produced, with posterior angles usually sharp (Figs. 84–88); ventral surface with sternites large, pigmented, and sclerotized. Head with 6 pigmented ocelli on each side ..... **Silphinae** ..... 2

2(1). Urogomphi longer than 10th abdominal segment by at least one-half their length (Figs. 79, 80). Sternum of second abdominal segment with 3 large sclerites (Fig. 73) ..... 3

Urogomphi equal to or only slightly longer than 10th abdominal segment (Figs. 78, 81–83). Sternum of second abdominal segment with 1 large sclerite (Fig. 74) ..... 5

3(2). Prothoracic tergite with anterior margin broadly and shallowly emarginate (Fig. 84); pale areas confined primarily to anterior one-half (Fig. 84). ..... ***Oxelytrum*** **Gistel***

Prothoracic tergite with anterior margin not emarginate (Figs. 85, 88); pale areas, if present, confined to lateral margins (Figs. 85, 88) ..... 4

4(3). Basal segment of urogomphus approximately two times, or less, as long as 10th abdominal segment (Fig. 80). Dorsal color primarily dark brown to black ..... ***Thanatophilus*** **Leach** (p. 40)
Basal segment of urogomphus more than twice as long as 10th abdominal segment (Fig. 79). Dorsal color primarily reddish brown ..... ***Necrodes*** **Leach** (p. 30)

5(2). Antenna with second segment having sensory area bearing 1 large cone (Fig. 75). Prothoracic tergite emarginate anteriorly at middle (Figs. 86, 87). Dorsum not black ..... ***Oiceoptoma*** **Leach** (p. 34)
Antenna with second segment having sensory area bearing 1, or more, plates (Figs. 76, 77). Prothoracic tergite not emarginate anteriorly. Dorsum predominantly or wholly dark brown or black ..... 6

6(5). Antenna with second and third segments equal in length. Urogomphus distinctly 2-segmented (Fig. 82) ..... ***Necrophila*** **Kirby & Spence** (p. 32)
Antenna with third segment distinctly longer than second segment. Urogomphus apparently with 1 segment (Figs. 78, 81) ..... 7

7(6). Antenna with second segment having sensory area bearing 1 plate (Fig. 77). Maxilla with apical segment of palpus approximately twice as long as wide ..... ***Aclypea*** **Reitter** (p. 24)
Antenna with second segment having sensory area bearing numerous plates (Fig. 76). Maxilla with apical segment of palpus approximately three times as long as wide ..... ***Heterosilpha*** **Portevin** (p. 28)

## Tableau de détermination des sous-familles et genres de Silphidae (larves) d'Amérique du Nord

1. Tergites petits, ceux de l'abdomen avec 4 épines (fig. 89); surface ventrale blanchâtre et molle, sans grands sternites. Tête avec 1 ocelle non pigmenté de chaque côté ..... **Nicrophorinae** ..... ***Nicrophorus*** **Fabricius** (p. 47)
Tergites grands, étendus latéralement, avec les angles postérieurs généralement distincts (fig. 84 à 88); surface ventrale avec des sternites grands, pigmentés et sclérifiés. Tête avec 6 ocelles pigmentés de chaque côté .. ***Silphinae*** ..... 2

2(1). Longueur des urogomphes au moins la moitié de celle du dixième segment abdominal (fig. 79 et 80). Sternum du deuxième segment abdominal avec 3 grands sclérites (fig. 73) ..... 3
Longueur des urogomphes égale ou légèrement supérieure à celle du dixième segment abdominal (fig. 78, 81 à 83). Sternum du deuxième segment abdominal avec 1 grand sclérite (fig. 74) ..... 5

3(2). Tergite prothoracique avec la marge antérieure échancrée en longueur mais non en profondeur (fig. 84); aires pâles restreintes surtout à la moitié antérieure (fig. 84) ..... ***Oxelytrum*** **Gistel***
Tergite prothoracique avec la marge antérieure non échancrée (fig. 85 et 88); aires pâles, si présentes, restreintes aux marges latérales (fig. 85 et 88) ..... 4

4(3). Article basal des urogomphes environ 2 fois plus long, ou moins, que le dixième segment abdominal (fig. 80). Couleur du dessus du corps surtout brun foncé à noir ..... ***Thanatophilus*** **Leach** (p. 40)

Article basal des urogomphes plus de 2 fois plus long que le dixième segment abdominal (fig. 79). Couleur du dessus du corps surtout brun rougeâtre ..... ***Necrodes*** **Leach** (p. 30)

5(2). Aire sensorielle du deuxième article antennaire avec 1 grand cône (fig. 75). Marge antérieure du tergite prothoracique échancrée au milieu (fig. 86 et 87). Dessus du corps non noir ..... ***Oiceoptoma*** **Leach** (p. 34)

Aire sensorielle du deuxième article antennaire avec 1 plaque ou plus (fig. 76 et 77). Marge antérieure du tergite prothoracique non échancrée. Dessus du corps en majeure partie ou totalement brun foncé ou noir .... 6

6(5). Deuxième et troisième articles antennaires de même longueur. Urogomphes distinctement formés chacun de 2 articles (fig. 82) ..... ..... ***Necrophila*** **Kirby & Spence** (p. 32)

Troisième article antennaire distinctement plus long que le deuxième. Urogomphes apparemment formés chacun d'un article (fig. 78 et 81) ..... 7

7(6). Aire sensorielle du deuxième article antennaire avec 1 plaque (fig. 77). Dernier article du palpe maxillaire environ 2 fois plus long que large ..... ..... ***Aclypea*** **Reitter** (p. 24)

Aire sensorielle du deuxième article antennaire avec plusieurs plaques (fig. 76). Dernier article du palpe maxillaire environ 3 fois plus long que large ..... ***Heterosilpha*** **Portevin** (p. 28)

## Subfamily Silphinae

### Genus *Aclypea* Reitter

*Aclypea* Reitter, 1884:81; Portevin 1926:61; Hatch 1928:93; Miller and Peck 1979:90; Madge 1980:354.

*Blitophaga* Reitter, 1884:82.

Recent study (Anderson and Peck 1984) has shown that two species of this Holarctic genus live in North America, and both have ranges in Canada and Alaska. Unlike other Nearctic silphids, the members of *Aclypea* are exclusively phytophagous. Adults can be recognized by the key characters, and also by the presence of a recurved metatibial spine in the males (Fig. 23). Adults range in length from 12 to 17 mm.

Larvae can be recognized by their black color, by the apparently one-segmented short urogomphi (Fig. 81), and by the sensory area of the second antennal segment bearing a single plate (Fig. 77). Although we have examined larvae from Alaska (presumably *A. opaca*) and Saskatchewan (presumably *A. bituberosa*), we cannot distinguish between them. Based on distributional data from adult specimens, it appears reasonable to treat larvae from the far north as *A. opaca* and those from elsewhere in North America as *A. bituberosa* until the problem is resolved.

## Key to species of adult *Aclypea* in North America

1. Genitalia of both sexes thinly sclerotized (light brown). Pronotum often with impunctate area on anterior third behind eye. Elytra with punctures shallow, the distance between punctures rarely less than the width of a puncture ..... ***A. opaca* (Linnaeus)** (p. 26)
Genitalia of both sexes thickly sclerotized (dark brown). Pronotum without impunctate area behind eye. Elytra with punctures deep, the distance between punctures often less than the width of a puncture ..... ***A. bituberosa* (LeConte)** (p. 25)

## Tableau de détermination des espèces d'*Aclypea* (adultes) d'Amérique du Nord

1. Génitalia des deux sexes finement sclérifiés (brun pâle). Pronotum souvent avec des aires lisses sur le tiers antérieur en arrière des yeux. Ponctuation des élytres peu profonde, la distance entre chaque point rarement inférieure à la largeur d'un point ..... ***A. opaca* (Linnaeus)** (p. 26)
Génitalia des deux sexes fortement sclérifiés (brun foncé). Pronotum sans aire lisse en arrière des yeux. Ponctuation des élytres profonde, la distance entre chaque point souvent inférieure à la largeur d'un point ..... ***A. bituberosa* (LeConte)** (p. 25)

### *Aclypea bituberosa* (LeConte)

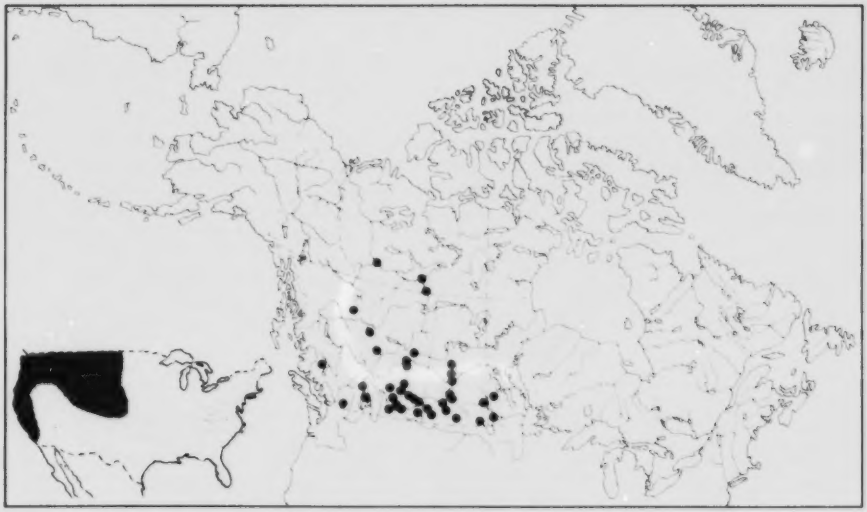
Figs. 3, 16, 23, 77, 81; Map 1

*Silpha bituberosa* LeConte, 1859*a*:6.
*Aclypea bituberosa*: Miller and Peck 1979:90.

**Diagnosis of adult**. Head and pronotum black to brown, usually covered with yellow to black pubescence, this abraded on some specimens. Pronotum with anterior margin usually thick, with lateral margins elevated; some specimens with impunctate areas present but with none behind eyes. Elytron tricostate, with punctures deep, often confluent, especially toward base. Isodiametric microsculpture of pronotum and elytra not distinct. Genitalia in both sexes thickly, darkly sclerotized. Length 14–17 mm.

**Distribution**. In Canada, this species is found throughout the Prairie Provinces, ranging north into the Northwest Territories and west into British Columbia. In the United States, it occurs throughout the northern Midwest into the western coastal and Rocky Mountain states.

Fossils of *A. bituberosa* 16 640 years B.P., have been found at Seattle, WA (Nelson, in litt.).



Map 1. Collection localities for *Aclypea bituberosa* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Natural history**. The natural history of this species has been documented by Cooley (1917). Adults and larvae are phytophagous, eating leaves and young shoots of *Chenopodium album*, *Monolepis nuttalliana*, and other native Chenopodiaceae, as well as *Solanum triflorum* (Solanaceae) (Hatch 1957; Cooley 1917). They have also been recorded from numerous cultivated crops (Anderson and Peck 1984) and are considered pests in some areas.

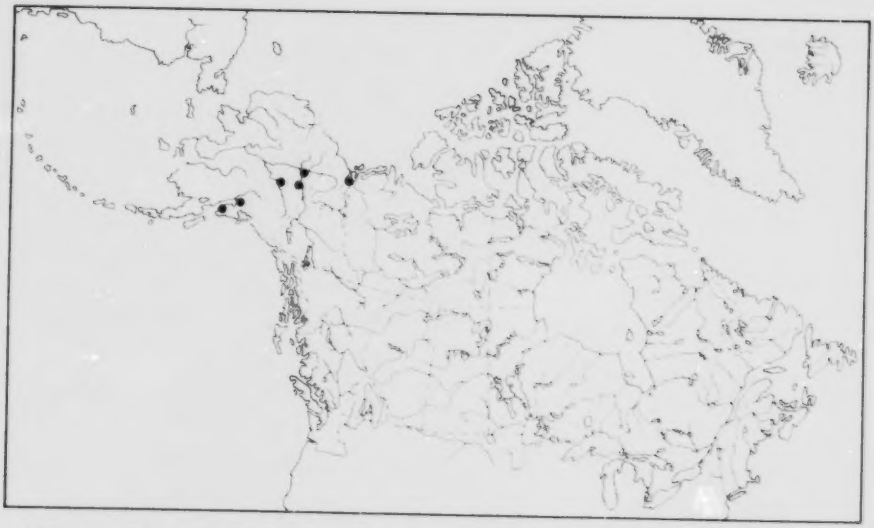
*A. bituberosa* is most often associated with grassland or prairie habitats. However, a few individuals have been collected in montane meadows. Adults are active from March through November, with later dates usually being more northerly or at high elevations.

**Geographic variation**. Although all adult prairie specimens of *A. bituberosa* are structurally similar, examination of the few available adult specimens from montane localities indicates a smaller overall size and much less convex elytra than those from lowland prairie areas. The punctation of the elytra also varies, becoming denser and with the punctures smaller and rarely confluent. These patterns of variation appear correlated with a change to montane–alpine habitats and may have an ecophenotypic basis.

### *Aclypea opaca* (Linnaeus)

Map 2

*Silpha opaca* Linnaeus, 1758:361.
*Aclypea opaca*: Miller and Peck 1979:90.



Map 2. Collection localities for *Aclypea opaca* in Canada and Alaska.

**Diagnosis of adult**. Head and pronotum black to brown, usually covered with yellow pubescence. Pronotum with anterior margin usually narrow, with lateral margins not distinctly raised; some specimens with impunctate areas present behind eyes. Elytron tricostate, usually pubescent, with punctures shallow, the distance between them rarely less than their width. Isodiametric microsculpture of pronotum and elytra distinct. Genitalia in both sexes thinly sclerotized, light brown. Length 12–15 mm.

**Distribution**. In North America, *A. opaca* is found only in Alaska and the extreme northwest of the Northwest Territories. It is also widely distributed in the Palearctic region (Hatch 1928).

**Natural history**. Little information is available on the natural history of this species in North America; however, the natural history of the species in Europe has been studied in detail by Martin (1945) and by Heymons et al. (1929). According to these authors, adults overwinter and emerge in spring when host plants (various Chenopodiaceae and some cultivated crops such as sugar beets) are germinating. Larvae appear about 2 weeks later and feed externally on young shoots and leaves. When mature, larvae move into the soil and pupate. Adults emerge 10–15 days later and they also feed on plants but not as extensively as larvae.

Nearctic records indicate that adults are active from June through August (Anderson and Peck 1984) and are probably associated with open habitats.

Mating behavior is similar to that noted for *Oiceoptoma noveboracense* (Heymons et al. 1929).

**Geographic variation.** None noted.

## Genus *Heterosilpha* Portevin

*Heterosilpha* Portevin, 1926:83; Miller and Peck 1979:92; Madge 1980:355.

Two species of this endemic North American genus are known. Only one has a distribution extending into Canada. Adults are characterized by the presence of a short row of erect hairs behind the eyes (Fig. 2), by the black pronotum, and by the elytra with reticulate sculpturing (Fig. 11). Adults range in length from 14 to 18 mm. Larvae are known only for *Heterosilpha ramosa* and these can be recognized by the key characters.

Matthews (1977) records a fossil of Miocene age from Meighen Island in the Canadian Arctic, which is assignable to the genus *Heterosilpha*. Close examination of this remarkably well preserved fossil reveals that the pronotum and elytron are not conspecific with either of the extant species: the punctures of the pronota of the extant forms are fine, whereas the fossil material bears large confluent punctures. Undoubtedly, the genus was more widely distributed in the past, when conditions in the far north were more amenable.

## Key to species of adult *Heterosilpha* in North America

1. Protarsal and mesotarsal segments 1–4 of males broadly expanded, densely pubescent beneath. Aedeagus thick, broad; parameres with apices thick, curved downward (Fig. 30). Females with each elytron drawn out at apex (Fig. 26). Elytra without metallic shinyness ..... ***H. ramosa* (Say)** (p. 29)

   Protarsal and mesotarsal segments of males not expanded, not densely pubescent beneath. Aedeagus thin, slender; parameres with apices narrow, straight (Fig. 29). Females with each elytron not drawn out at apex. Elytra of some specimens with metallic shinyness ..... ***H. aenescens* (Casey)***

*Distributed in coastal California and southern Oregon.

## Tableau de détermination des espèces d'*Heterosilpha* (adultes) d'Amérique du Nord

1. Articles 1 à 4 des protarses et mésotarses des mâles très dilatés, densément pubescents en dessous. Édéage épais, large; apex des paramères épais, courbé vers le bas (fig. 30). Chaque élytre des femelles prolongé à l'apex (fig. 26). Élytres sans lustre métallique ... ***H. ramosa* (Say)** (p. 29)

Articles des protarses et mésotarses des mâles non dilatés, non densément pubescents en dessous. Édéage mince, étroit; apex des paramères étroit et droit (fig. 29). Chaque élytre des femelles non prolongé à l'apex. Élytres de certains spécimens avec un lustre métallique ..... ..... ***H. aenescens*** **(Casey)***

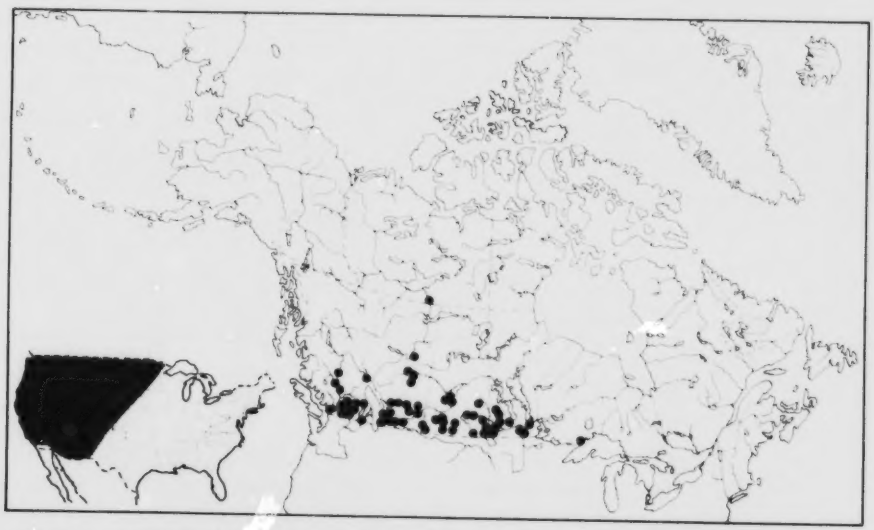
*Espèce répartie sur la côte de la Californie et dans le sud de l'Orégon.

## *Heterosilpha ramosa* (Say)

Figs. 14, 26, 30, 76, 78; Map 3

*Silpha ramosa* Say, 1823:193.
*Silpha cervaria* Mannerheim, 1843:252.
*Heterosilpha ramosa*: Portevin 1926:148.

**Diagnosis of adult**. Pronotum black, finely densely punctate. Elytron tricostate, black, not metallic. Males with protarsal and mesotarsal segments 1–4 laterally expanded, densely pubescent beneath. Females with elytral apices prolonged (Fig. 26). Moderately sized beetles, 14–18 mm long.



Map 3. Collection localities for *Heterosilpha ramosa* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of larva.** Dorsum uniformly dark brown to black; some specimens with midline pale; tergites only slightly produced laterally. Antenna with sensory area of second segment bearing numerous small irregularly arranged plates (Fig. 76). Urogomphus one-segmented, slightly shorter than 10th abdominal segment (Fig. 78). Sternum of second abdominal segment with single large sclerite (as in Fig. 74).

Larvae have also been described by Gissler (1880), Dorsey (1940), and Brewer and Bacon (1975).

**Distribution.** In Canada, this species is primarily found in the south, from extreme northwestern Ontario and Manitoba, west to coastal British Columbia. It is also widely distributed in the western United States (Miller and Peck 1979).

**Natural history.** The natural history of *H. ramosa* in Colorado has been discussed by Brewer and Bacon (1975). Their study shows that adults overwinter and become active in mid-April of the following year. Mating takes place, and eggs are laid in soil around a carcass. There are two generations each year with the second peak of adult activity in late July through early August. The egg-to-adult period takes about 30 days; the egg stage lasts 5 days, the first instar 4–5 days, the second instar 5–6 days, the third instar 8–10 days, and the pupal stage 8–9 days. Observations are also given on mating behavior and feeding habits.

Other studies on the natural history of this species include those by Gissler (1880) and Goe (1919), the latter erroneously referring to it as *Oiceoptoma inaequale*. Linsley (1942) records *H. ramosa* as feeding on dead grasshoppers in California, but it is possible that these observations refer to *H. aenescens*.

*H. ramosa* appears to be most common in aspen parkland habitats that characterize prairie–forest interfaces.

**Geographic variation.** None noted.

## Genus *Necrodes* Leach

*Necrodes* Leach, 1815:88; Portevin 1926:159; Hatch 1928:122; Madge 1980:356.
*Asbolus* Bergroth, 1884:229.
*Protonecrodes* Portevin, 1922:508.

One species of the genus *Necrodes* is found in North America. Adults and larvae can readily be distinguished from all other North American silphids by the key characters.

### *Necrodes surinamensis* (Fabricius)

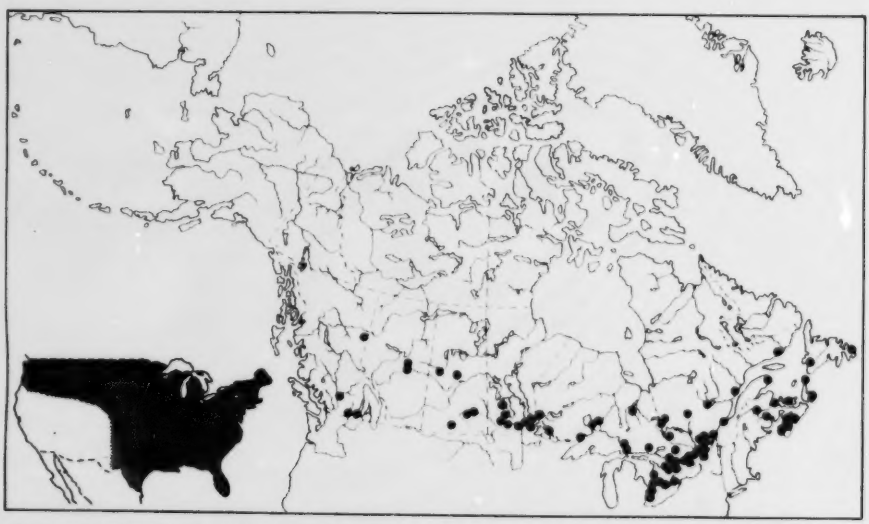
Figs. 4, 12, 15, 17, 20, 73, 79, 85; Map 4

*Silpha surinamensis* Fabricius, 1775:72.
*Protonecrodes surinamensis bizonatus* Portevin, 1926:165.
*Necrodes surinamensis*: Leach 1815:88.

**Diagnosis of adult.** Eyes large. Labrum shallowly emarginate (Fig. 4). Pronotum black, orbicular, widest near middle, narrowly explanate (Fig. 15). Elytron tricostate, black with red markings in apical one-quarter (Fig. 12); some specimens with red markings along lateral margin near midline. Males with hind femora often greatly expanded. Length 15–25 mm.

**Diagnosis of larva.** Dorsum dark reddish brown; thoracic and abdominal tergites each with lateral margins and midline pale creamy white, slightly produced laterally (Fig. 85). Antenna with sensory area on second segment bearing large sensory cone (as in Fig. 75). Urogomphus two-segmented, approximately 2.5 times length of 10th abdominal segment; first segment four times length of second segment (Fig. 79). Venter with sternum of second abdominal segment divided into 3 large sclerites (Fig. 73).

Larvae have been described in detail by Wickham (1895), Dorsey (1940), and Ratcliffe (1972).



Map 4. Collection localities for *Necrodes surinamensis* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution**. In Canada, this species is found in the south from Newfoundland and Nova Scotia, west to British Columbia, though apparently only locally common in the west. It is also widely distributed in the United States; also recorded doubtfully from South America (Portevin 1926; Hatch 1928; Ratcliffe 1972).

**Natural history**. The natural history of this species in Nebraska has been documented by Ratcliffe (1972). The adults emerge early in April. Mating and oviposition ensue, and eggs are laid in the soil surrounding a carcass. Upon hatching, 2–4 days later, the young larvae move to the carcass to feed. The first instar (treated by Ratcliffe as two distinct instars) may last from 3 to 15 days, the second from 3 to 20 days, and the third from 3 to 5 days, though all larval instars can be prolonged by periods of adversity. There is a 5–8-day prepupal period, and the pupal period lasts 12–17 days. It is the adult stage that overwinters. It was not ascertained how many generations there are each year, but this may vary with geographic locality. In Canada and the northeastern United States, there is probably only one period of reproductive activity a year (Anderson 1982*a*).

Adults of this species are nocturnal and often caught at lights. They are found on larger carcasses (for example, dog, bear, moose, deer), and it is these larger carcasses that appear to be solely used for reproductive purposes. Because larger carcasses are used, food resources may not be a limiting factor, and this may contribute to the wide distribution of the species.

Mite relationships, behavior, natural enemies, and other aspects of its natural history are discussed by Ratcliffe (1972).

Eisner and Meinwald (1982) discuss the chemical composition of a rectal gland secretion in *N. surinamensis* that appears to be used by the adult beetles to defend themselves.

**Geographic variation**. There is much variation in elytral patterns of adults of this species (Ratcliffe 1972: Fig. 30). In some adult specimens the elytra are immaculate, whereas in others two transverse red bands, or rows, of red spots are present. There has been no attempt at correlating these patterns with geographic locality.

## Genus *Necrophila* Kirby & Spence

*Necrophila* Kirby and Spence, 1828:509; Portevin 1926:148; Hatch 1928:101; Madge 1980:356.
*Necrobora* Hope, 1840:151.
*Necrotropha* Gistel, 1848:121.

A single species of this Holarctic genus is known to occur in North America. Adults are characterized by a short row of erect hairs behind the eyes (Fig. 2); a large fovea on the frons, midway between the eyes (Fig. 2);

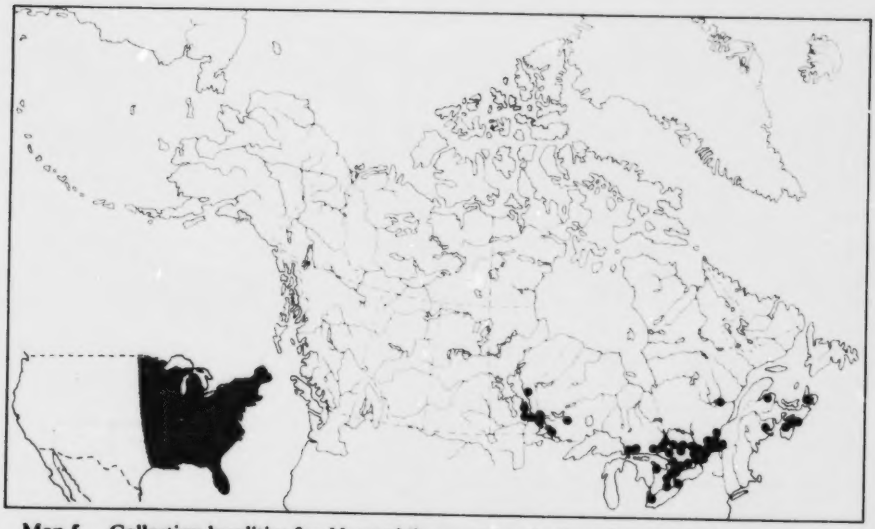
a pronotum with disc black, margins yellow; and elytra with reticulate sculpturing (Fig. 11). Adults range in size from 15 to 20 mm long. Larvae can be recognized by their black color; short two-segmented urogomphi (Fig. 82); sternum of second abdominal segment with single sclerite (Fig. 74); and sensory area of second antennal segment bearing numerous plates (Fig. 76).

### *Necrophila americana* (Linnaeus)

Figs. 2, 11, 27, 82; Map 5

*Silpha americana* Linnaeus, 1758:360.
*Silpha peltata* Catesby, 1771:Pl. 10, Fig. 7.
*Oiceoptoma terminata* Kirby, 1837:103.
*Oiceoptoma affine* Kirby, 1837:103.
*Oiceoptoma canadensis* Kirby, 1837:104.
*Necrophila americana*: Kirby and Spence 1828:509.

**Diagnosis of adult.** Pronotum with margins yellow, disc black. Elytron tricostate, black, with reticulate sculpturing (Fig. 11). Females with elytral apices prolonged, males not so (Fig. 27). Larger beetles, 15–20 mm long.



Map 5. Collection localities for *Necrophila americana* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of larva.** Dorsum black, midline in some specimens pale; tergites only slightly produced laterally. Antenna with sensory area of second segment bearing numerous small irregularly arranged plates (as in Fig. 76). Urogomphus two-segmented, length approximately equal to or slightly longer than 10th abdominal segment; first segment approximately 4–4.5 times length of second segment (Fig. 82). Sternum of second abdominal segment with single large sclerite (as in Fig. 74).

Larvae have been described in detail by Dorsey (1940).

**Distribution.** This species is found in southern Canada from Nova Scotia west to central Manitoba. It is also widely distributed in the eastern United States.

**Natural history.** *N. americana* adults breed in late spring and early summer, with the first adults appearing during the latter part of May in Ontario (Anderson 1982*a*), New York (Pirone 1974), and New Jersey (Shubeck 1976). In more southerly areas, adult emergence occurs in late March (Reed 1958).

Reproduction occurs from late May through mid-July, with most larval emergence occurring from late May to mid-June (Anderson 1982*a*). There is only one generation each year with an egg-to-adult duration of approximately 10–12 weeks. Overwintering takes place in the adult stage.

The species is found primarily in mesic, open habitats (Anderson 1982*a*) but also in forested areas (Shubeck 1969; Pirone 1974; Walker 1957). Adults have been recorded as being primarily diurnal (Shubeck 1971).

Mating behavior is similar to that noted for *Oiceoptoma noveboracense*.

**Geographic variation.** Specimens from southern localities (e.g., Arkansas, Alabama, and Georgia) tend to be much more oval than northern specimens. The elytral apices, which are tipped with yellow in northern areas, are uniformly black in southern populations. Variation in size and shape of the black pronotal spot has also been recorded (Hatch 1927*a*).

## Genus *Oiceoptoma* Leach

*Oiceoptoma* Leach, 1815:89; Portevin 1926:89; Hatch 1928:89; Madge 1980:357.
*Oeceoptoma* Agassiz, 1847:256.

Three species of this genus are found in North America, two of which have distributions extending into the study area. Adults are characterized by the presence of a short row of long erect hairs behind the eyes (Fig. 2), widely separated mesocoxae, and toothed elytral shoulders (Fig. 22). Adults of North American species range from 12 to 15 mm long. Females have the

sutural apices of the elytra prolonged to sharp points, whereas the males have the apices broadly rounded (Fig. 25).

Larvae can be recognized by their predominantly reddish brown dorsal coloration, with the lateral margins of the tergites strongly produced and at least partly whitish (Figs. 86, 87); short, two-segmented urogomphi (Fig. 83); and sensory area of second antennal segment bearing a large cone (Fig. 75).

## Key to species of adult *Oiceoptoma* in North America

1. Pronotum with disc black, margins orange red ..... ***O. noveboracense* (Forster)** (p. 38)
   Pronotum with disc and margins black ..... 2
2(1). Elytron with epipleuron wide in posterior half, and with upper oblique portion twice width of lower vertical portion (Fig. 31); elytral intervals smooth ..... ***O. inaequale* (Fabricius)** (p. 36)
   Elytron with epipleuron narrow, and with upper oblique portion approximately equal in width to lower vertical portion throughout length (Fig. 32); elytral intervals in some specimens with transverse rugose sculpturing ..... ***O. rugulosum* Portevin***

*Distributed in southeastern and south central United States.

## Tableau de détermination des espèces d'*Oiceoptoma* (adultes) d'Amérique du Nord

1. Pronotum avec le disque noir, les marges orangé rouge ..... ***O. noveboracense* (Forster)** (p. 38)
   Pronotum avec le disque et les marges noirs ..... 2
2(1). Épipleure de l'élytre large dans la moitié postérieure, avec la partie oblique supérieure 2 fois plus large que la partie verticale inférieure (fig. 31); interstries des élytres lisses ..... ***O. inaequale* (Fabricius)** (p. 36)
   Épipleure de l'élytre étroit, avec la partie oblique supérieure à peu près de même largeur que la partie verticale inférieure sur toute la longueur (fig. 32); interstries des élytres, chez certains spécimens, avec une sculpture transverse rugueuse ..... ***O. rugulosum* Portevin***

*Espèce répartie dans le sud-ouest et le centre-sud des États-Unis.

## Key to species of known larval *Oiceoptoma* in North America

1. Thoracic tergites and abdominal tergites 1–8 with lateral margins mostly pale, marked with small oblique dark spots or lines (Fig. 86); prothoracic tergite deeply emarginate anteriorly (Fig. 86) ..... ***O. noveboracense* (Forster)** (p. 38)

Mesothoracic, metathoracic, and abdominal tergites 1–8 with pale areas confined to posterolateral angles (Fig. 87); prothoracic tergite with both anterolateral and posterolateral angles pale, shallowly emarginate anteriorly (Fig. 87) ..... ***O. inaequale*** **(Fabricius)** (p. 36)

## Tableau de détermination des espèces d'*Oiceoptoma* (larves connues) d'Amérique du Nord

1. Tergites thoraciques et abdominaux 1 à 8 avec les marges latérales surtout pâles, avec de petites taches ou lignes obliques foncées (fig. 86); bord antérieur du tergite prothoracique très échancré (fig. 86) ..... ..... ***O. noveboracense*** **(Forster)** (p. 38)

   Tergites mésothoracique, métathoracique et abdominaux 1 à 8 avec des aires pâles restreintes aux angles postérolatéraux (fig. 87); tergite prothoracique avec les angles antérolatéraux et postérolatéraux pâles, son bord antérieur légèrement échancré (fig. 87) ..... ..... ***O. inaequale*** **(Fabricius)** (p. 36)

### *Oiceoptoma inaequale* (Fabricius)

Figs. 31, 87; Map 6

*Silpha inaequalis* Fabricius, 1781:87.
*Oiceoptoma inaequale*: Kirby 1837:102.

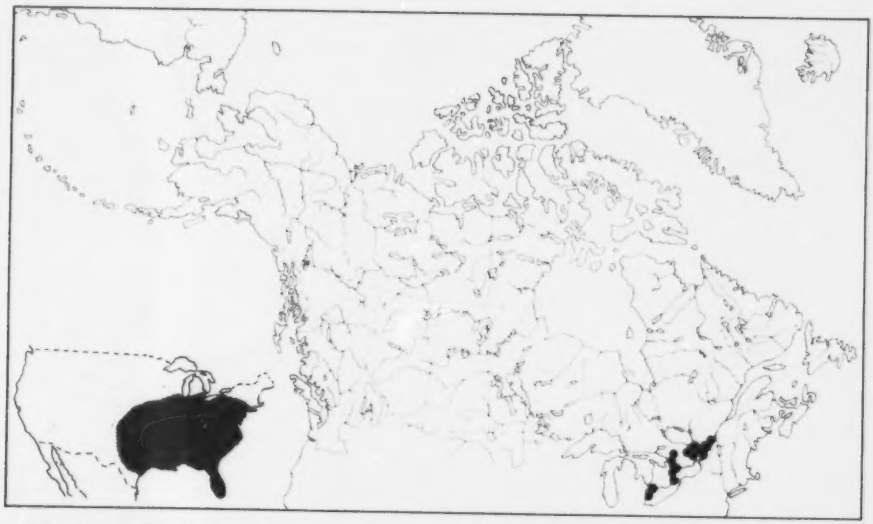
**Diagnosis of adult.** Head and pronotum black, covered with fine black pubescence. Elytron tricostate, black, with intervals flat; elytral epipleuron wide in posterior half (Fig. 31). Length 13–15 mm.

**Diagnosis of larva.** Dorsum largely light to dark reddish brown; mesothoracic, metathoracic, and abdominal tergites 1–8 with pale areas confined to posterolateral angles and also the midline in some specimens (Fig. 87); prothoracic tergite with pale areas in both anterolateral and posterolateral angles as well as midline in some specimens, shallowly emarginate anteriorly (Fig. 87). Antenna with sensory area of second segment bearing large cone (as in Fig. 75). Urogomphi two-segmented, equal to 10th abdominal segment in length; first segment approximately 2.5 times length of second segment (as in Fig. 83). Sternum of second abdominal segment composed of single sclerite (as in Fig. 74).

Larvae have been described in detail by Dorsey (1940).

**Distribution.** In Canada, this species occurs in extreme southern Ontario and Quebec. It is widely distributed in the eastern United States.

**Natural history.** Adults of *O. inaequale* are reproductively active in the early spring. In Ontario (Anderson 1982*a*) and in New Jersey (Shubeck



Map 6. Collection localities for *Oiceoptoma inaequale* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

1976) the first adults appear from late April to late May. In more southerly localities such as Maryland (Howden 1950) and Tennessee (Reed 1958), adults first appear in early to mid-February. *O. inaequale* is rare or absent in more northerly localities but becomes more common throughout the central and southern part of its range.

There appears to be one generation each year (Reed 1958; Howden 1950; Anderson 1982*a*) with egg laying occurring during May in the north and during February and March in the south. Overwintering is accomplished in the adult stage. Data are not available on details of life history, but observations of Cole (1942) indicate an egg duration of 7 days and a larval duration of 20 days. These data combined with the seasonal data of Shubeck (1976) indicate a pupal period of 2–3 weeks.

The species appears restricted to deciduous forest habitats, though it has been recorded from some unforested areas (Cole 1942). Observations on seasonal activity by Cole indicate that adult *O. inaequale* are active on carcasses before both *O. noveboracense* and *Necrophila americana* in areas where all three occur together. The different times of reproductive activity and the habitat preferences of *N. americana* and *O. inaequale* should minimize competitive interactions between these two species, whose ranges are broadly overlapping. A broad zone of sympatry exists between *O. noveboracense* and *O. inaequale*, but one of the two species always appears to be locally rare or absent.

Shubeck (1971) indicates that adults are primarily diurnal.

**Geographic variation**. None noted.

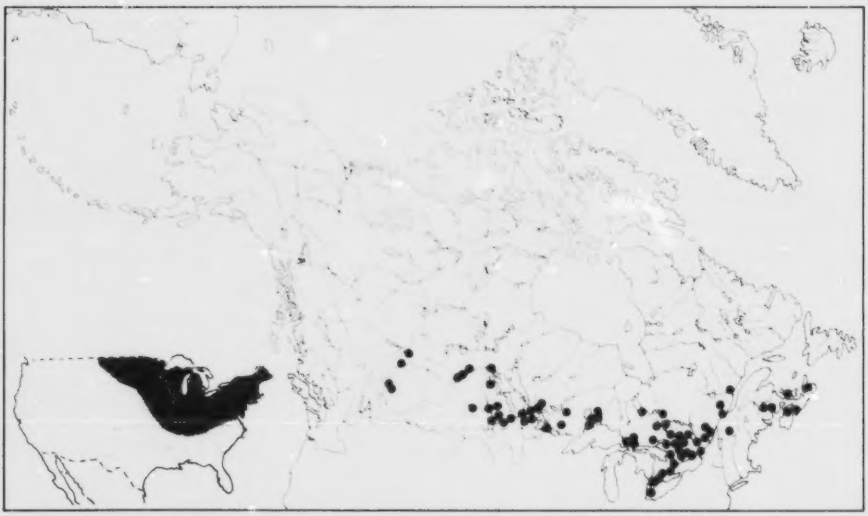
### *Oiceoptoma noveboracense* (Forster)

Figs. 22, 25, 74, 75, 83, 86; Map 7

*Silpha noveboracensis* Forster, 1771:17.
*Silpha marginalis* Fabricius, 1776:215.
*Oiceoptoma marginata* Kirby, 1837:100.
*Oiceoptoma novoboracensis*: Portevin 1926:93 (unjustified emendation).

**Diagnosis of adult**. Head and disc of pronotum black; margins of pronotum orange red. Elytron tricostate, brownish to black; intervals flat. Length 13–15 mm.

**Diagnosis of larva**. Dorsum largely light to dark reddish brown; thoracic tergites and abdominal tergites 1–8 with lateral margins pale, and with small oblique dark markings (Fig. 86); midline of some specimens also pale. Prothoracic tergite deeply emarginate anteriorly (Fig. 86). Antenna with sensory area of second segment bearing a large cone (Fig. 75). Urogomphi



Map 7. Collection localities for *Oiceoptoma noveboracense* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

two-segmented, equal to 10th abdominal segment in length; first segment approximately 2.5 times length of second segment (Fig. 83). Sternum of second abdominal segment composed of single large sclerite (Fig. 74).

Larvae have been described in detail by Dorsey (1940).

**Distribution**. In Canada, this species occurs in the southern areas from Alberta east to the Atlantic coast. It is quite common in the east but only locally common in the west. It is also widespread in the northeastern United States.

**Natural history**. Adults of this species are reproductively active in spring, with the first adults appearing in mid-April in Ontario (Anderson 1982*a*), New York (Pirone 1974), and New Jersey (Shubeck 1976). In more southerly areas emergence occurs earlier, with the first adults appearing in late February in Tennessee (Reed 1958) and Maryland (Howden 1950). In more northern localities it is the dominant early season silphine of forested areas where *O. inaequale* is usually rare or absent. Throughout the central part of its range, where both *O. inaequale* and *O. noveboracense* occur, one of the two species is usually locally rare, but even so, adults of the former precede the latter in emergence by a few days to weeks (Cole 1942; Howden 1950; Reed 1958). In southern areas *O. noveboracense* is absent and *O. inaequale* is the dominant spring species, whereas in extreme southern areas such as Florida, Louisiana, and Texas, a third species, *O. rugulosum*, is often the sole species present.

In the north there is one generation each year. Mating and egg laying occur from mid-April to late May. Individual females lay 8–10 eggs in soil surrounding a carcass. Based on both field and laboratory observations, the egg stage lasts 5–6 days, the first instar 4–5 days, the second instar 7–8 days, and the third instar 10 days, whereupon the larvae dig into the soil and pupate. No pupae were observed, though seasonal data (Anderson 1982*a*) indicate a generation period of 6–8 weeks, thereby suggesting 2–3 weeks spent in pupal development. Teneral adults appear in July, and overwintering is in the adult stage.

*O. noveboracense* is most commonly found in forested habitats. This, combined with its period of reproductive activity, minimizes interactions with other species with which it could be associated.

Adults have been recorded as being primarily diurnal (Shubeck 1971).

In the early spring, before and during the mating season, adults of this species are commonly found paired, with males mounted on top of females. This position is apparently maintained for sustained periods of time, though copulation is not actively occurring. A closer examination usually reveals that the male has one of the antennae of the female firmly grasped in his mandibles. This position is maintained until copulation occurs. At this time the male releases the antenna of the female and moves backward on her elytra. He uses his antennae to drum or stroke the pronotum of the female while

attempting copulation. Once copulation has terminated, the male returns to his original position on the female, once again grasping one of her antennae in his mandibles. This pattern of behavior continues until the female lays eggs. When eggs or larvae are present, few pairs are seen in this position. It appears that this behavior terminates at oviposition and may be a method by which males insure their reproductive investment (see Alcock 1979; Parker 1970). Similar behavior also occurs in *Necrophila americana* (personal observation) and *Aclypea opaca* (Heymons et al. 1929), and may be indicative of a relationship between these three genera. Observations of *Thanatophilus lapponicus* indicate that similar behavior does not occur in this species.

**Geographic variation.** None noted.

## Genus *Thanatophilus* Leach

*Thanatophilus* Leach, 1815:89; Portevin 1926:28; Hatch 1928:79; Madge 1980:359; Schawaller 1981:1.
*Pseudopelta* Bergroth, 1884:229.
*Philas* Portevin, 1903:331.

Five species of *Thanatophilus* are found in North America, four of which have distributions extending into the study area. Adults of the genus are characterized by lack of a short row of long erect hairs behind the eyes, small eyes, shallowly emarginate labrum, and widely separated mesocoxae. They are smaller (8–15 mm long), often possessing pubescence on the dorsal surface of the pronotum. Females of most species have the sutural apices of the elytra prolonged and rounded, whereas the males have the apices rounded but not prolonged (Fig. 28). The world species have been reviewed by Schawaller (1981).

Larvae can be recognized by their dark brown to black color; urogomphi longer than 10th abdominal segment (Fig. 80); and the sternum of second abdominal segment bearing 3 large sclerites (Fig. 73).

## Key to species of adult *Thanatophilus* in North America

1. Elytron without costae (Fig. 10) ..... ***T. truncatus* (Say)***
   Elytron with costae (Figs. 6–9) ..... 2
2(1). Elytron with tubercles interspersed between the costae (Fig. 7) ..... ***T. lapponicus* (Herbst)** (p. 43)
   Elytron without tubercles between the costae (Figs. 6, 8, 9) ..... 3
3(2). Elytron with inner two costae effaced near base (Fig. 6). Pronotum without pubescence. Eighth abdominal segment orange ..... ***T. coloradensis* (Wickham)** (p. 42)

*Distributed in the southwestern United States and northern Mexico.

Elytron with inner two costae entire (Figs. 8, 9). Pronotal pubescence grayish. Eighth abdominal segment black ..... 4

4(3). Elytron with outer costa extending beyond apical callus (Fig. 9). Pronotal postcoxal lobe pointed (Fig. 18) ..... ***T. sagax*** **(Mannerheim)** (p. 41)

Elytron with outer costa terminating at apical callus (Fig. 8). Pronotal postcoxal lobe rounded (Fig. 19) .... ***T. trituberculatus*** **(Kirby)** (p. 46)

## Tableau de détermination des espèces de *Thanatophilus* (adultes) d'Amérique du Nord

1. Élytre sans costae (fig. 10) ..... ***T. truncatus*** **(Say)***

Élytre avec des costae (fig. 6 à 9) ..... 2

2(1). Élytre avec des tubercules intercallés entre les costae (fig. 7) ..... ***T. lapponicus*** **(Herbst)** (p. 43)

Élytre sans tubercules entre les costae (fig. 6, 8 et 9) ..... 3

3(2). Élytre avec les deux costae internes effacées vers la base (fig. 6). Pronotum sans pubescence. Huitième segment abdominal orangé ..... ***T. coloradensis*** **(Wickham)** (p. 42)

Élytre avec les deux costae internes entières (fig. 8 et 9). Pronotum avec une pubescence grisâtre. Huitième segment abdominal noir ..... 4

4(3). Élytre avec la costa externe prolongée au delà du calus apical (fig. 9). Lobe postcoxal du pronotum pointu (fig. 18) ..... ***T. sagax*** **(Mannerheim)** (p. 41)

Élytre avec la costa externe cessant au calus apical (fig. 8). Lobe postcoxal du pronotum arrondi (fig. 19) ..... ***T. trituberculatus*** **(Kirby)** (p. 46)

*Espèce répartie dans le sud-ouest des États-Unis et dans le nord du Mexique.

## Key to species of known larval *Thanatophilus* in North America

1. Thoracic tergites and abdominal tergites 1–9 uniformly black (except for midline, which is pale in some specimens) ***T. lapponicus*** **(Herbst)** (p. 43)

Thoracic tergites and abdominal tergites 1–9 with lateral margins yellowish (Fig. 88), otherwise black ..... ***T. coloradensis*** **(Wickham)** (p. 42)

## Tableau de détermination des espèces de *Thanatophilus* (larves connues) d'Amérique du Nord

1. Tergites thoraciques et abdominaux 1 à 9 uniformément noirs (à l'exception de la ligne médiane qui est pâle chez certains spécimens) ..... ***T. lapponicus*** **(Herbst)** (p. 43)

Tergites thoraciques et abdominaux 1 à 9 avec les marges latérales jaunâtres (fig. 88), le reste noir ..... ***T. coloradensis*** **(Wickham)** (p. 42)

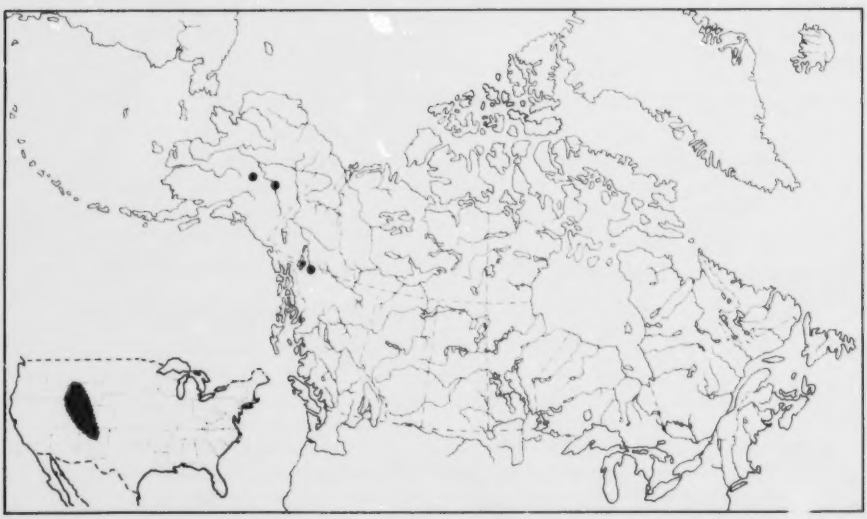
## *Thanatophilus coloradensis* (Wickham)

Figs. 6, 80, 88; Map 8

*Silpha coloradensis* Wickham, 1902:180.
*Thanatophilus obalskii* Portevin, 1920:507.
*Thanatophilus coloradensis*: Portevin 1926:43.

**Diagnosis of adult.** Head and pronotum black, lacking pubescence, evenly, densely punctate. Pronotal postcoxal lobe pointed. Sternal pubescence sparse, brown. Elytron tricostate, black; intervals flat; the inner two costae effaced near base (Fig. 6). Last abdominal segment orange. Length 11–14 mm.

**Diagnosis of larva.** Dorsum dark brown to black; thoracic tergites and abdominal tergites 1–9 with lateral margins yellowish (Fig. 88), only slightly produced laterally; some specimens with midline pale creamy white. Antenna with sensory area of second segment bearing large cone (as in Fig. 75). Urogomphus two-segmented, approximately 1.5 times length of 10th abdominal segment; first segment three times length of second segment (Fig. 80). Sternite of second abdominal segment bearing 3 large sclerites (as in Fig. 73).



Map 8. Collection localities for *Thanatophilus coloradensis* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution.** This species has been collected in central Alaska and northern British Columbia. It is also found at high elevations above the tree line in Colorado, New Mexico, Utah, Montana, and Wyoming.

Matthews (1975, 1979) records fossils of this species from the Yukon Territory and Alaska, 80 000–30 000 years B.P.

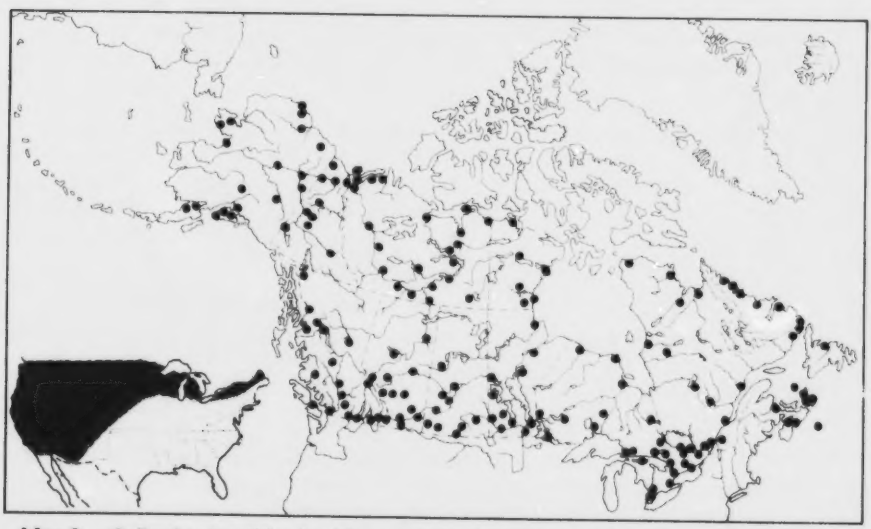
**Natural history.** Very little is known of the natural history of this species. We have caught large series of adults in carrion-baited pitfall traps in rocky alpine tundra at elevations of 3962 m in the areas mentioned under Distribution. It probably feeds and reproduces on carcasses of the common burrowing alpine rodents.

Information on the natural history and distribution of *T. coloradensis* is given in more detail in Peck and Anderson (1982).

**Geographic variation.** None noted.

*Thanatophilus lapponicus* (Herbst)

Figs. 7, 28; Map 9



Map 9. Collection localities for *Thanatophilus lapponicus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

*Silpha lapponica* Herbst, 1793:209.
*Silpha caudata* Say, 1823:192.
*Silpha tuberculata* Germar, 1824:81.
*Silpha californica* Mannerheim, 1843:253.
*Thanatophilus lapponicus*: Portevin 1926:33.

**Diagnosis of adult**. Head and pronotum black, covered with dense gray pubescence. Pronotal postcoxal lobe broadly rounded. Sternal pubescence dense, gray. Elytron tricostate, black; intervals tuberculate (Fig. 7). Length 10–14 mm.

**Diagnosis of larva**. Dorsum uniformly dark brown to black; some specimens with midline pale creamy white. Tergites only slightly produced laterally. Antenna with sensory area of second segment bearing large cone (as in Fig. 75). Urogomphus two-segmented, approximately two times length of 10th abdominal segment; first segment two times length of second segment. Sternite of second abdominal segment composed of 3 sclerites (as in Fig. 73).

Larvae have been described in detail by Dorsey (1940).

**Distribution**. *T. lapponicus* is widely distributed in Canada and Alaska. In the United States, it is found primarily in the north, but in the west it ranges south to California, New Mexico, Arizona, and Mexico. This species is also widely distributed in the Palearctic region (Hatch 1928).

**Natural history**. Adults of *T. lapponicus* are reproductively active in the early spring, with the first adults appearing in late April in Ontario (Anderson 1982*a*). It is the dominant species of open habitats throughout its range, particularly in northern areas, where it is often the sole silphid collected.

In Ontario (Anderson 1982*a*), there are two generations each year. The first mating and egg-laying occurs from late April to late May. In early June, tenerals are present in the population and soon thereafter mating and egg-laying occur again, continuing throughout late July. Teneral adults are present until early September, when the numbers of adults begin to decrease. This appears to indicate overwintering in the adult stage.

Individual females lay approximately 10 eggs in soil around a carcass. Based solely on field observations, the egg stage lasts 5–6 days, the first instar about 7 days, the second instar 8–10 days, and the third instar 10–12 days. No pupae were observed.

*T. lapponicus* is a cold-adapted species that in the west occurs at high elevations in mountains, and ranges south into California and New Mexico. Throughout most of its range in northern Canada and Alaska it occurs with *T. sagax* and *T. trituberculatus*, two rare species for which there is little natural history information. It also occurs with *T. coloradensis* in Alaska, but this last named species appears to be extremely rare there. This situation

appears to have been reversed in the late Pleistocene, when *T. coloradensis* was dominant in interior Alaska (Matthews 1975, 1979) and *T. lapponicus* was rare or absent. In other northern areas, *T. sagax* and *T. trituberculatus* are the only silphid fossils recorded during these late Pleistocene periods (Matthews 1968, 1974*a*; Ashworth, in litt.; Elias, pers. com. 1983; Harington 1980; Morgan, in litt.; Nelson, in litt.). The lack of fossils of *T. lapponicus* appears odd in view of its present distribution, natural history, and abundance. This may be the result of qualitative changes in the tundra ecosystem during the Pleistocene as proposed by Matthews (1974*b*, 1979). Detailed study of the natural history of *T. sagax* and *T. trituberculatus* would certainly contribute to a better understanding of the situation.

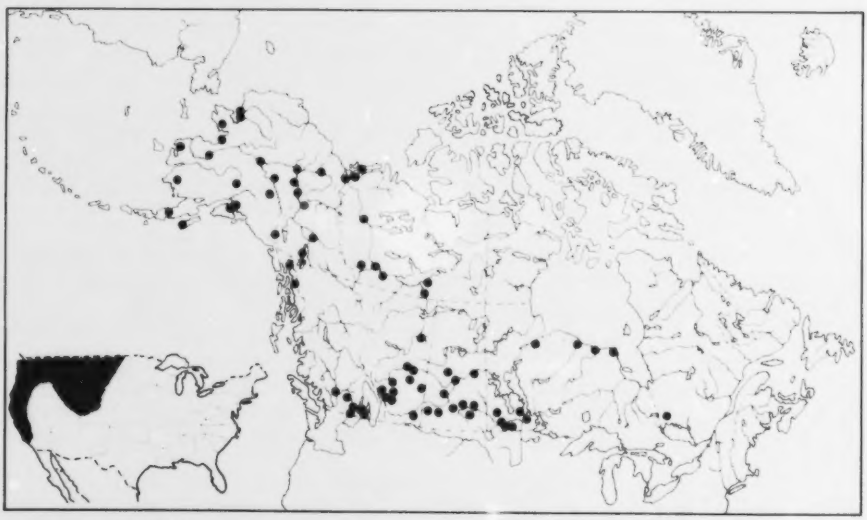
In Europe and Asia, *T. lapponicus* has been regarded as an injurious pest to furs, meats, and dried fish (Emetz 1975).

**Geographic variation**. None noted.

### *Thanatophilus sagax* (Mannerheim)

Figs. 9, 18; Map 10

*Silpha sagax* Mannerheim, 1853:173.
*Thanatophilus sagax*: Portevin 1926:138.



Map 10. Collection localities for *Thanatophilus sagax* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of adult.** Head and pronotum black, covered with short gray pubescence. Pronotal postcoxal lobe pointed (Fig. 18). Sternal pubescence moderately dense, brown. Elytron tricostate, black; intervals flat; outer elytral costa extending beyond apical callus (Fig. 9). Length 10–13 mm.

**Distribution.** This species is widely distributed in the north, from Alaska south to southern British Columbia and east to eastern Quebec. In the United States, it is found in the west from Washington south to California (Hatch 1957 as *T. trituberculatus*); and in the north central states from North Dakota south into Colorado.

Matthews (1968, 1974*a*), Harington (1980), Nelson, in litt., and Morgan, in litt., record fossils of *T. sagax* from interior Alaska of ages 24 000, 8000–4000, 6400, 9600, and 700 years B.P., respectively.

**Natural history.** This species is primarily northern and like most other members of the genus in North America appears to be cold-adapted. As with *T. trituberculatus*, most adult specimens have been found under debris or carrion along shores of lakes, alkali sloughs, and rivers; it seems that these are sites of reproductive activity. Specimen data indicate adult activity from May to September.

**Geographic variation.** None noted.

### *Thanatophilus trituberculatus* (Kirby)

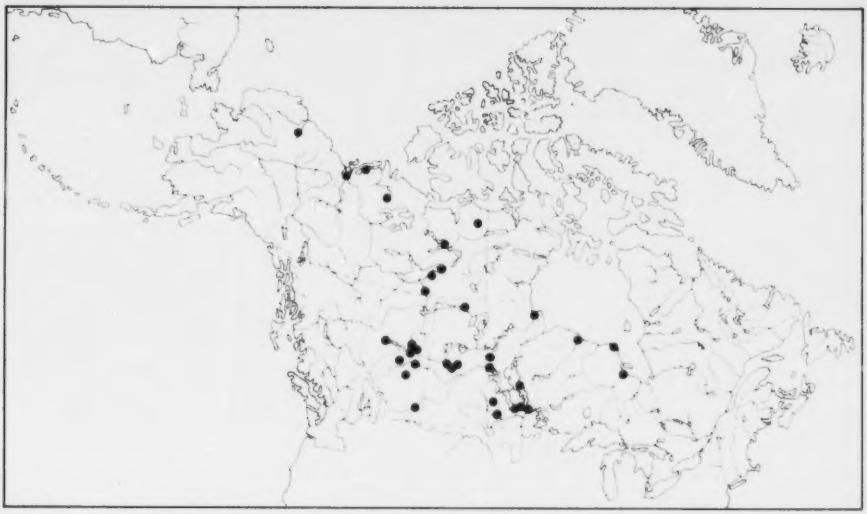
Figs. 8, 19; Map 11

*Oiceoptoma trituberculatum* Kirby, 1837:101.
*Thanatophilus trituberculatus*: Portevin 1926:48.

**Diagnosis of adult.** Head and pronotum black, covered with short gray pubescence. Pronotal postcoxal lobe rounded (Fig. 19). Sternal pubescence moderately dense, brown. Elytron tricostate, black; intervals flat; outer elytral costa ending at apical callus (Fig. 8). Length 8–11 mm.

**Distribution.** This species is found in central Canada from southern Saskatchewan, Alberta, and Manitoba north into the Northwest Territories, west to Alaska, and east to Ontario. We have not seen any specimens from the United States, though Hatch (1957) and Hatch and Reuter (1934) record it from the Pacific Northwest. These most likely represent *T. sagax*, a more widely distributed species that is often confused with *T. trituberculatus*. Hatch (1927*b*) also records it from Minnesota, and although this may be a valid record of *T. trituberculatus*, there is the possibility of it referring to *T. sagax*.

Fossils of *T. trituberculatus* have been recorded from Sibley County, MN, 13 000 years B.P. (Ashworth, in litt.) and Ennadai Lake, Keewatin, N.W.T., 5500 years B.P. (Elias, pers. com. 1983). The record of Ashworth is from a pioneering assemblage that colonized southern Minnesota after the



Map 11. Collection localities for *Thanatophilus trituberculatus* in Canada and Alaska.

retreat of Wisconsinan ice, and indicates that *T. trituberculatus* survived Wisconsinan glaciation south of the ice sheet.

**Natural history**. This species is primarily northern and appears to be cold-adapted. Adult specimens are most often found on carrion and under debris along lakeshores and riversides. Larvae and adults have been collected under washed-up detritus along lake margins, indicating that these are sites of reproduction. Specimen data indicate that adults are active from May to August.

**Geographic variation**. None noted.

## Subfamily Nicrophorinae

### Genus *Nicrophorus* Fabricius

*Nicrophorus* Fabricius, 1775:71; Portevin 1926:181; Hatch 1928:126; Madge 1980:357.
*Necrophorus* Thunberg, 1789:7.
*Necrophagus* Leach, 1815:88.
*Cyrtoscelis* Hope, 1840:149.
*Acanthopsilus* Portevin, 1914:223.

*Necrocharis* Portevin, 1923:141.
*Necroxenus* Semenov-Tian-Shanskij, 1926:46.
*Eunecrophorus* Semenov-Tian-Shanskij, 1933:152.
*Necrocleptes* Semenov-Tian-Shanskij, 1933:153.
*Necrophorindus* Semenov-Tian-Shanskij, 1933:153.
*Necrophoriscus* Semenov-Tian-Shanskij, 1933:152.
*Nesonecrophorus* Semenov-Tian-Shanskij, 1933:153.
*Necropter* Semenov-Tian-Shanskij, 1933:154.
*Nesonecropter* Semenov-Tian-Shanskij, 1933:154.
*Stictonecropter* Semenov-Tian-Shanskij, 1933:154.
*Neonicrophorus* Hatch, 1946:99.

There are 15 species of this widespread genus in North America, north of Mexico, 14 of which occur in Canada. Adults are easily characterized by their truncate elytra, which are usually marked with red or orange (frontispiece). They are distinct and easily recognized members of our fauna. Males of most species can be recognized by their asymetrical and laterally expanded foretarsal segments (Fig. 44*a*). In females the foretarsal segments are usually only slightly symetrically and laterally expanded (Fig. 44*b*). In some species the sexes are difficult to distinguish on external characters.

Larvae are easily recognized by their extremely reduced sclerotization and by the quadrispinose abdominal tergites (Fig. 89). Keys to larvae presented here are from Anderson (1982*b*).

*Nicrophorus* has always been a popular group among coleopterists and this has led to a great number of nomenclatorial problems, particularly regarding subgeneric concepts and intraspecific variation. Until phylogenetic relationships can be established among species of *Nicrophorus*, use of the subgeneric names proposed by Semenov-Tian-Shanskij (1926, 1933), Portevin (1923, 1926), and Hatch (1946) should be avoided. Our preliminary analysis of relationships indicates that these names do not represent natural groupings. Similarly, names proposed for intraspecific variants, whether nomenclatorially valid (i.e., subspecies) or not (i.e., race or variety) should be avoided. Analyses of geographic variation in those species, where it is extensive (Anderson and Peck, unpublished data), indicate that distribution of variable characters (primarily the color pattern of elytra) within and between populations is inconsistent with application of formal subspecific names (see Mayr 1969; Kavanaugh 1979 for criteria for subspecies recognition).

## Key to species of adult *Nicrophorus* in North America

1. Pronotum without anterior transverse impression, lateral margins extremely narrow (Fig. 43). Elytral epipleuron narrow (Fig. 55) ..... ..... ***N. carolinus* (Linnaeus)** (p. 55)
Pronotum with anterior transverse impression, lateral margins not narrow (Figs. 39–42). Elytral epipleuron wide (Fig. 45) ..... 2

2(1). Frons and pronotal disc red. Tarsal empodium quadrisetose (Fig. 33) ... ..... *N. americanus* **Olivier** (p. 54)

Frons and pronotal disc black. Tarsal empodium bisetose (Fig. 34) ... 3

3(2). Pronotum with dense yellow pubescence ..... ..... *N. tomentosus* **Weber** (p. 70)

Pronotum glabrous, or with sparse hair on anterior or lateral ..... margins ..... 4

4(3). Posterior lobe of metepimeron (Fig. 5) with dense yellow pubescence; pronotum cordate (Fig. 42) ..... 5

Posterior lobe of metepimeron glabrous, or with dark hairs or only a few yellow hairs; pronotum variable (Figs. 39–41) ..... 7

5(4). Anterior face of procoxa with short hairs on basal half ..... ..... *N. marginatus* **Fabricius** (p. 63)

Anterior face of procoxa with long hairs on basal half ..... 6

6(5). Penultimate antennal segment with outer edge deeply emarginate (Fig. 35); basal segment of antennal club black. Elytron with anterior black band reaching epipleural ridge but not crossing onto epipleuron (Figs. 71, 72) ..... *N. obscurus* **Kirby** (p. 65)

Penultimate antennal segment with outer edge shallowly emarginate (Fig. 36); basal segment of antennal club black or orange; if orange, elytron with anterior black band crossing onto epipleuron (Fig. 65); if black, the elytral maculations reduced or absent (Figs. 67–69) ..... ..... *N. guttula* **Motschulsky** (p. 58)

7(4). Metatibia curved. Anterior black band of elytron not reaching epipleuron (Fig. 47) ..... *N. sayi* **Laporte** (p. 69)

Metatibia straight. Anterior black band of elytron usually reaching epipleuron (Figs. 45, 46, 51) ..... 8

8(7). Elytral epipleuron unicolorous, black or orange ..... 9

Elytral epipleuron bicolored, black and orange (Figs. 49–51) ..... 13

9(8). Elytral epipleuron black ..... 10

Elytral epipleuron orange ..... 12

10(9). Dorsal surface of elytron with long fine hairs. Epipleural ridge short, reaching only to level of tip of scutellum (Fig. 45) ..... ..... *N. orbicollis* **Say** (p. 66)

Dorsal surface of elytron without long hairs. Epipleural ridge long, reaching almost to level of base of scutellum (Fig. 46) ..... 11

11(10). Elytron immaculate, entirely black. Metasternal pubescence brown, long, dense ..... *N. nigrita* **Mannerheim** (p. 64)

Elytron maculate, with 1 small anterolateral spot and 2 small posterior spots (Fig. 46). Metasternal pubescence yellow brown, sparse ..... ..... *N. pustulatus* **Herschel** (p. 68)

12(9). Metasternum with elongate bald patch immediately posterior to each mesocoxa (Fig. 5). Elytron with continuous multiple and irregular rows of stout, erect hairs around shoulder to base of epipleural ridge (Fig. 37) ..... *N. hybridus* **Hatch & Angell** (p. 60)

Metasternum without bald patches immediately posterior to each mesocoxa. Elytron with continuous multiple and irregular rows of hairs around shoulder but ending well before base of epipleural ridge (Fig. 38); elytral maculations often greatly reduced (Figs. 59–62) ..... ..... *N. investigator* **Zetterstedt** (p. 61)

13(8). Metasternal pubescence brown; apical three segments of antennal club red ..... *N. mexicanus* **Matthews***

*Distributed in the southwestern United States and Mexico.

Metasternal pubescence yellow; apical three segments of antennal club black ..... 14

14(13). Base of elytral epipleuron orange, with prebasal black spot (Figs. 49, 50). Upper and lower faces of ninth and 10th antennal segments each with patch of dense white hairs arranged in "figure eight" pattern ..... ..... *N. vespilloides* **Herbst** (p. 72)

Base of elytral epipleuron entirely black (Fig. 51). Upper and lower faces of ninth and 10th antennal segments without dense white hairs, though vestige of the "figure eight" pattern may be present ..... ..... *N. defodiens* **Mannerheim** (p. 56)

## Tableau de détermination des espèces de *Nicrophorus* (adultes) d'Amérique de Nord

1. Pronotum sans impression transverse antérieure, les marges latérales très étroites (fig. 43). Épipleure de l'élytre étroit (fig. 55) ..... ..... *N. carolinus* **(Linnaeus)** (p. 55)

Pronotum avec une impression transverse antérieure, les marges latérales non étroites (fig. 39 à 42). Épipleure de l'élytre large (fig. 45) ..... 2

2(1). Front et disque du pronotum rouges. Empodium tarsal avec 4 soies (fig. 33) ..... *N. americanus* **Olivier** (p. 54)

Front et disque du pronotum noirs. Empodium tarsal avec 2 soies (fig. 34) ..... 3

3(2). Pronotum avec une pubescence jaune dense ..... ..... *N. tomentosus* **Weber** (p. 70)

Pronotum glabre ou avec des soies éparses sur la marge antérieure ou les marges latérales ..... 4

4(3). Lobe postérieur du métépimère (fig. 5) avec une pubescence jaune dense; pronotum cordiforme (fig. 42) ..... 5

Lobe postérieur du métépimère glabre, ou avec des soies foncées ou avec quelques soies jaunes seulement; pronotum de forme variable (fig. 39 à 41) ..... 7

5(4). Face antérieure du procoxa avec de courtes soies sur la moitié basale ... ..... *N. marginatus* **Fabricius** (p. 63)

Face antérieure du procoxa avec de longues soies sur la moitié basale ... ..... 6

6(5). Pénultième article antennaire avec le bord externe profondément échancré (fig. 35); article basal de la massue antennaire noir. Bande antérieure noire de l'élytre atteignant la carène épipleurale, mais pas l'épipleure (fig. 71 et 72) ..... *N. obscurus* **Kirby** (p. 65)

Pénultième article antennaire avec le bord externe légèrement échancré (fig. 36); article basal de la massue antennaire noir ou orangé; si orangé, bande antérieure noire de l'élytre atteignant l'épipleure (fig. 65); si noir, taches élytrales réduites ou absentes (fig. 67 et 69) ..... ..... *N. guttula* **Motschulsky** (p. 58)

7(4). Métatibia courbé. Bande antérieure noire de l'élytre n'atteignant pas l'épipleure (fig. 47) ..... *N. sayi* **Laporte** (p. 69)

Métatibia droit. Bande antérieure noire de l'élytre atteignant le plus souvent l'épipleure (fig. 45 à 46, 51) ..... 8

8(7). Épipleure de l'élytre unicolore, noir ou orangé ..... 9
Épipleure de l'élytre bicolore, noir et orangé (fig. 49 à 51) ..... 13
9(8). Épipleure de l'élytre noir ..... 10
Épipleure de l'élytre orangé ..... 12
10(9). Surface dorsale de l'élytre avec de longues et fines soies. Carène épipleurale courte, atteignant seulement le niveau de la pointe du scutellum (fig. 45) ..... *N. orbicollis* **Say** (p. 66)
Surface dorsale de l'élytre sans longue soies. Carène épipleurale longue, atteignant presque le niveau de la base du scutellum (fig. 46) ..... 11
11(10). Élytre sans taches, complètement noir. Pubescence du métasternum brune, longue et dense ..... *N. nigrita* **Mannerheim** (p. 64)
Élytre maculé avec 1 petite tache antérolatérale et 2 petites taches postérieures (fig. 46). Pubescence du métasternum brun jaune, éparse ..... *N. pustulatus* **Herschel** (p. 68)
12(9). Métasternum avec une région dénudée, allongée et postérieure à chaque mésocoxa (fig. 5). Élytre avec des rangées continuelles, multiples et irrégulières, de grosses soies droites autour de l'épaule jusqu'à la base de la carène épipleurale (fig. 37) ..... *N. hybridus* **Hatch & Angell** (p. 60)
Métasternum sans région dénudée postérieure à chaque mésocoxa. Élytre avec des rangées de soies continuelles, multiples et irrégulières autour de l'épaule, mais se terminant bien en avant de la base de la carène épipleurale (fig. 38); taches élytrales souvent très réduites (fig. 59 à 62) ..... *N. investigator* **Zetterstedt** (p. 61)
13(8). Pubescence du métasternum brune; trois articles apicaux de la massue antennaire rouges ..... *N. mexicanus* **Matthews***
Pubescence du métasternum jaune; trois articles apicaux de la massue antennaire noirs ..... 14
14(13). Base de l'épipleure de l'élytre orangée, avec une tache prébasale noire (fig. 49 et 50). Faces supérieure et inférieure des neuvième et dixième articles antennaires avec une zone de soies blanches denses formant un motif « figure huit » ..... *N. vespilloides* **Herbst** (p. 72)
Base de l'épipleure de l'élytre entièrement noire (fig. 51). Faces supérieure et inférieure des neuvième et dixième articles antennaires sans soies blanches denses, bien qu'un vestige du motif « figure huit » peut être présent ..... *N. defodiens* **Mannerheim** (p. 56)

*Espèce répartie dans le sud-ouest des États-Unis et au Mexique.

## Key to species of known larval *Nicrophorus* in North America

1. Venter of 10th abdominal segment unsclerotized at base (Fig. 91); sternite of ninth abdominal segment truncate at lateral margins (Figs. 94, 95), or else fragmented (Fig. 96) ..... 2
Venter of 10th abdominal segment sclerotized at base (Figs. 90–92); sternite of ninth abdominal segment entire, with posterior margin straight, and with anterior margin broadly arcuate, emarginate at middle (Fig. 93) .. 4
2(1). Sternite of ninth abdominal segment fragmented (Fig. 96) ..... *N. marginatus* **Fabricius** (p. 63)

Sternite of ninth abdominal segment entire, with lateral margins truncate (Figs. 94, 95) ..... 3

3(2). Middorsal and lateral spines of tergite of third abdominal segment equal in length ..... ***N. obscurus*** **Kirby** (p. 65)

Middorsal spines of tergite of third abdominal segment approximately three times length of lateral spines ..... ***N. guttula*** **Motschulsky** (p. 58)

4(1). Labial palpus with first segment unsclerotized ventrally (Fig. 98); distance between bases of labial palpi approximately one-half width of first segment of palpus (Fig. 98) ..... 5

Labial palpus with first segment sclerotized ventrally (Fig. 97); distance between bases of labial palpi twice width of first segment of palpus (Fig. 97) ..... 6

5(4). Bases of urogomphi lacking sutures where they join tergite. Middorsal spines of tergites of abdominal segments 2–8 at least twice as long as lateral spines ..... ***N. defodiens*** **Mannerheim*** (p. 56)

Bases of urogomphi with sutures often incomplete at middle where they join tergite. Middorsal spines of tergites of only abdominal segments 4–8 at least twice as long as lateral spines ..... ***N. sayi*** **Laporte** (p. 69)

6(4). Tenth abdominal segment sclerotized mid-ventrally in apical half, the sclerite Y-shaped, extending to bases of innermost pair of apical setae (Fig. 92) ..... 7

Tenth abdominal segment unsclerotized mid-ventrally in apical half (Fig. 90) ..... 8

7(6). Lateral spines of tergites of abdominal segments 3–8 approximately one-half length of middorsal spines; lateral spines of tergite of ninth abdominal segment large, with distance to base of urogomphus from base of lateral spine equal to length of lateral spine ..... ***N. investigator*** **Zetterstedt** (p. 61)

Lateral spines of tergites of only seventh and eighth abdominal segments approximately one-half length of middorsal spines; lateral spines of tergite of ninth abdominal segment smaller, with distance to base of urogomphus from base of lateral spine equal to twice length of lateral spine ..... ***N. nigrita*** **Mannerheim** (p. 64)

8(6). Lateral and middorsal spines of tergites of first abdominal segment equal in length; middorsal spines of tergites of abdominal segments 2–8 at least twice as long as lateral spines; lateral spines of tergites of abdominal segments 1–8 small, not exceeding diameter of spiracle ..... ***N. tomentosus*** **Weber** (p. 70)

Lateral spines of tergites of abdominal segments 1–3 slightly longer or equal to length of middorsal spines; middorsal spines of tergites of only abdominal segments 4–8 at least twice as long as lateral spines; lateral spines of tergites of abdominal segments 1–8 large, approximately twice diameter of spiracle on segments 6–8 ..... 9

9(8). Lateral spines of tergite of ninth abdominal segment large, with distance to base of urogomphus from base of lateral spine approximately equal to length of lateral spine ..... ***N. hybridus*** **Hatch & Angell** (p. 60)

Lateral spines of tergite of ninth abdominal segment minute, appearing only as small cones, with distance to base of urogomphus from base of lateral spine 4 times, or more, length of lateral spine ..... ***N. orbicollis*** **Say** (p. 66)

*Characters of larvae of *Nicrophorus vespilloides* discussed by Pukowski (1934) and Hatch (1927*a*) indicate that this species will key to *N. defodiens* in this key. Unfortunately, we have not seen larvae of *N. vespilloides* and therefore cannot distinguish between it and *N. defodiens*.

## Tableau de détermination des espèces de *Nicrophorus* (larves connues) d'Amérique de Nord

1. Surface ventrale du dixième segment abdominal non sclérifiée à la base (fig. 91); sternite du neuvième segment abdominal avec les marges latérales tronquées (fig. 94 et 95) ou sternite fragmenté (fig. 96) ..... 2

Surface ventrale du dixième segment abdominal sclérifiée à la base (fig. 90 à 92); sternite du neuvième segment abdominal entier, avec la marge postérieure droite, et avec la marge antérieure très arquée et échancrée au milieu (fig. 93) ..... 4

2(1). Sternite du neuvième segment abdominal fragmenté (fig. 96) ..... ***N. marginatus*** **Fabricius** (p. 63)

Sternite du neuvième segment abdominal entier, avec les marges latérales tronquées (fig. 94 et 95) ..... 3

3(2). Épines dorsales et latérales du troisième tergite abdominal de même longueur ..... ***N. obscurus*** **Kirby** (p. 65)

Épines dorsales du troisième tergite abdominal environ 3 fois plus longues que les épines latérales ..... ***N. guttula*** **Motschulsky** (p. 58)

4(1). Premier article du palpe labial non sclérifié ventralement (fig. 98); distance entre la base de chaque palpe labial environ moitié moins grande que la largeur du premier article du palpe (fig. 98) ..... 5

Premier article du palpe labial sclérifié ventralement (fig. 97); distance entre la base de chaque palpe labial 2 fois plus grande que la largeur du premier article du palpe (fig. 97) ..... 6

5(4). Base des urogomphes sans suture au niveau de la jonction avec le tergite. Épines dorsales des tergites abdominaux 2 à 8 au moins 2 fois plus longues que les épines latérales ..... ***N. defodiens*** **Mannerheim*** (p. 56)

Base des urogomphes avec des sutures, souvent incomplètes au milieu, au niveau de la jonction avec le tergite. Épines dorsales des tergites abdominaux 4 à 8 au moins 2 fois plus longues que les épines latérales .. ..... ***N. sayi*** **Laporte** (p. 69)

6(4). Face ventrale du dixième segment abdominal sclérifiée au milieu sur la moitié apicale; le sclérite en forme de Y, prolongé jusqu'à la base de la paire de soies apicales la plus interne (fig. 92) ..... 7

Face ventrale du dixième segment abdominal non sclérifiée au milieu sur la moitié apicale (fig. 90) ..... 8

7(6). Épines latérales des tergites abdominaux 3 à 8 environ moitié moins longues que les épines dorsales; épines latérales du neuvième tergite abdominal grandes, la distance de la base des épines latérales jusqu'à la base des urogomphes égale à la longueur de l'épine latérale ..... ***N. investigator*** **Zetterstedt** (p. 61)

Épines latérales des septième et huitième tergites abdominaux environ moitié moins longues que les épines dorsales; épines latérales du neuvième tergite abdominal plus courtes, la distance de la base des épines latérales jusqu'à la base des urogomphes égale à 2 fois la longueur de l'épine latérale ..... ***N. nigrita*** **Mannerheim** (p. 64)

*Les caractères de la larve de *Nicrophorus vespilloides* étudiée par Pukowski (1934) et Hatch (1927*a*) indiquent que cette espèce se placerait dans le tableau de détermination auprès de *N. defodiens*. Malheureusement, nous n'avons pas examiné de larves de *N. vespilloides* et, par conséquent, nous ne pouvons les distinguer de celles de *N. defodiens*.

8(6). Épines latérales et dorsales du premier tergite abdominal de même longueur; épines dorsales des tergites abdominaux 2 à 8 au moins 2 fois plus longues que les épines latérales; épines latérales des tergites abdominaux 1 à 8 petites, n'excédant pas le diamètre d'un stigmate ..... ***N. tomentosus*** **Weber** (p. 70)

Épines latérales des tergites abdominaux 1 à 3 légèrement plus longues ou de même longueur que les épines dorsales; épines dorsales des tergites abdominaux 4 à 8 au moins 2 fois plus longues que les épines latérales; épines latérales des tergites abdominaux 1 à 8 larges et environ 2 fois le diamètre d'un stigmate sur les segments 6 à 8 ..... 9

9(8). Épines latérales du neuvième tergite abdominal grandes, la distance de la base des épines latérales jusqu'à la base des urogomphes à peu près égale à la longueur de l'épine latérale ..... ***N. hybridus*** **Hatch & Angell** (p. 60)

Épines latérales du neuvième tergite abdominal minuscules, ressemblant à de petits cônes, la distance de la base des épines latérales jusqu'à la base des urogomphes 4 fois, ou plus, la longueur de l'épine latérale ..... ***N. orbicollis*** **Say** (p. 66)

## *Nicrophorus americanus* Olivier

Figs. 33, 48; Map 12

*Nicrophorus americanus* Olivier, 1790:6.
*Nicrophorus virginicus* Frölich, 1792:123.
*Necrophorus grandis* Fabricius, 1801:247.

**Map 12. Collection localities for *Nicrophorus americanus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.**

**Diagnosis of adult**. Pronotum orbicular, with lateral and basal margins broad and with anterior transverse impression well-defined (as in Fig. 39). Pronotal disc and frons red. Antennal club orange. Metasternal pubescence yellow brown; metepimeron with pubescence sparse, brown. Hind tibia slightly curved. Tarsal empodium quadrisetose (Fig. 33). Elytron with pattern as in Fig. 48. This is the largest North American *Nicrophorus*, with adults reaching lengths of 25–35 mm.

**Distribution**. In Canada, this species is known from few localities in extreme southern Ontario and Quebec. In the United States, it was once widely distributed in the eastern states but now appears restricted to isolated localities (Anderson 1982*c*; Davis 1980).

**Natural history**. Although *N. americanus* is one of the most distinctive and commonly recognized members of our fauna, virtually nothing has been published on its natural history. Adults have been recorded at carrion in Tennessee (Walker 1957) and Ohio (Jacques 1915). Adults were also the subject of some crude experiments on olfactory senses (Abbott 1927*a*).

Inferences have been made (Anderson 1982*c*) on its natural history based on its large size and what is known of the natural history of other large *Nicrophorus*. We believe its decline over the past 50 years to be attributable to ecological factors associated with this large size and to the deforestation of eastern North America, which has removed mature climax forests from all but a few isolated localities.

Adults are nocturnal, and most specimens have been caught at light traps and not at carrion.

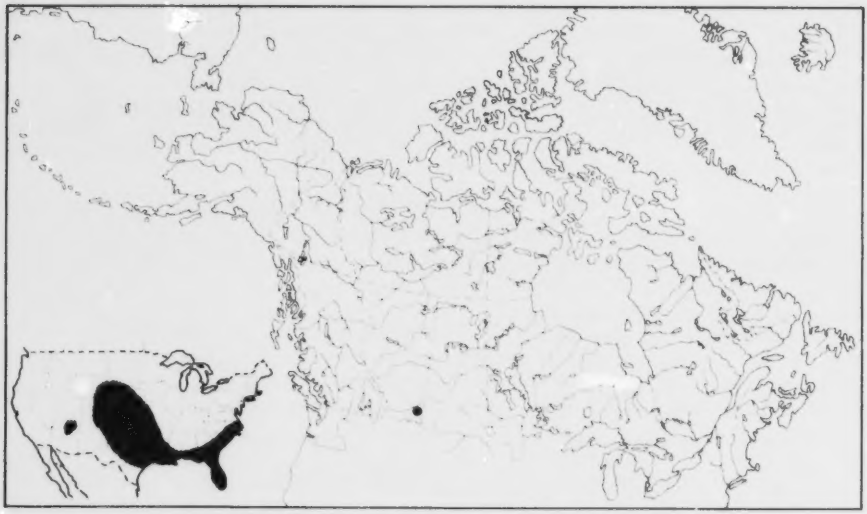
**Geographic variation**. None noted.

### *Nicrophorus carolinus* (Linnaeus)

Figs. 43, 55, 56; Map 13

*Silpha carolina* Linnaeus, 1771:530.
*Necrophorus mediatus* Fabricius, 1801:334.
*Necrophorus mysticallis* Angell, 1912:307.
*Necrophorus carolinus scapulatus* Portevin, 1923:142.
*Necrophorus carolinus dolosus* Portevin, 1923:307.
*Necrophorus carolinus*: Horn 1880:228.

**Diagnosis of adult**. Pronotum cordate, with lateral margins extremely narrow except at base; basal margins moderately wide; anterior transverse impression lacking (Fig. 43). Antennal club orange. Metasternal pubescence yellow, and metepimeron glabrous. Hind tibia slightly curved. Elytral epipleuron extremely narrow (Fig. 55). Elytron with pattern as in Figs. 55, 56. Moderately sized, 15–20 mm long.



Map 13. Collection localities for *Nicrophorus carolinus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution**. In Canada, this species is known from a single specimen from southeast Alberta. It is widespread in the United States, from the central states south to Texas and Arizona, east along the Gulf Coastal Plain to Florida, then north along the Atlantic Coastal Plain to Virginia.

**Natural history**. Arnett (1946) observed adults of this species burying a dead snake. *N. carolinus* appears restricted to sandy soil in open or sparsely forested areas. No other data on natural history are available.

**Geographic variation**. The typical elytral color pattern (Fig. 55) is the most common throughout the southeastern portion of its range. In the north central states, the maculations are discontinuous and reduced (Fig. 56). A population at Tuba City, AZ, contains many individuals that are entirely black.

### *Nicrophorus defodiens* Mannerheim

Figs. 1, 24, 51–54, 90, 93; Map 14

*Necrophorus defodiens* Mannerheim, 1846:513.
*Necrophorus pollinctor* LeConte, 1854:19.
*Necrophorus conversator* Walker, 1866:320.
*Necrophorus plagiatus* Motschulsky, 1869:352.

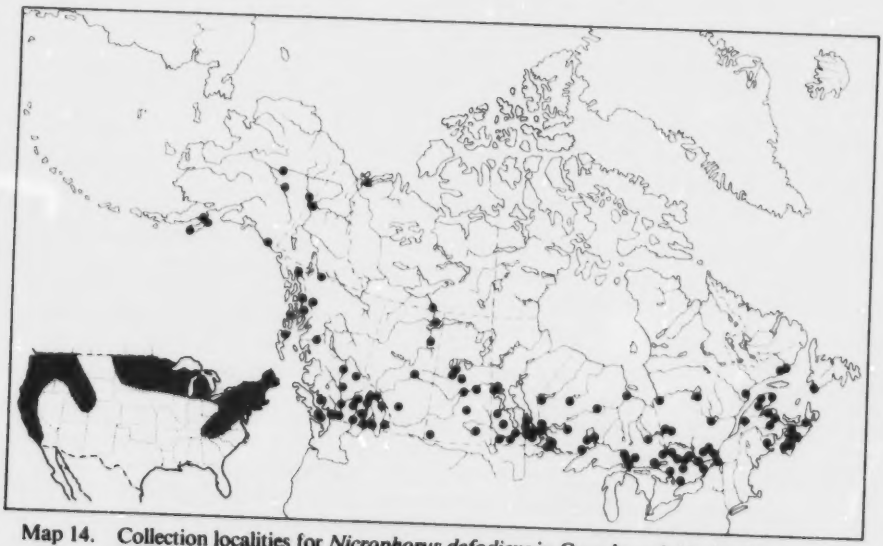
*Necrophorus defodiens binotatus* Portevin, 1926:236.
*Necrophorus defodiens kadjakensis* Portevin, 1926:236.
*Necrophorus defodiens mannerheimi* Portevin, 1926:236.

**Diagnosis of adult**. Pronotum quadrate, with wide lateral and basal margins (as in Fig. 40). Antenna with club entirely black; vestige of the "figure eight" pattern of white hairs may be present as in *N. vespilloides*. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibia straight. Elytron with pattern variable (Figs. 51–54). Smaller in size, 12–18 mm long.

**Diagnosis of larva**. Labial palpi narrowly separated, with basal segment unsclerotized ventrally (as in Fig. 98). Ninth abdominal segment with sternite entire (Fig. 93); 10th abdominal segment with base sclerotized ventrally (Fig. 90). Middorsal spines of tergites of abdominal segments 2–8 at least twice as long as lateral spines. Urogomphus with suture at base lacking.

**Distribution**. This species is widely distributed in Canada and Alaska. It is also found in the western coastal and Rocky Mountain states, and in the north central and eastern states, south along the Appalachian Mountains to Tennessee and North Carolina.

**Natural history**. The pattern of seasonal development is similar to that of *N. vespilloides* in Ontario (Anderson 1982*a*). *N. defodiens* is found primarily in the dry boreal forest throughout its range but also occurs in montane and coastal forests of British Columbia and the coastal states.



Map 14. Collection localities for *Nicrophorus defodiens* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

Adults of *N. defodiens* do not bury carcasses but conceal them under leaf litter or debris. Details of the life history of this species are presented by Leech (1934).

Adults are crepuscular throughout the range of the species.

**Geographic variation.** Variation in elytral patterns of adults of this species are extensive (Figs. 51–54), and many forms can be represented in a single brood (Leech 1934). The normally maculated form (Fig. 51), which characterizes inland and eastern coastal areas, grades into melanistic forms in western coastal areas. Elytral maculations in individuals from western coastal areas vary from slight reduction (Fig. 52) to great reduction in size and an increase in fragmentation (Fig. 54). Some adults in coastal areas may be entirely black.

Melanism in coastal areas has been well-documented for Lepidoptera by Hovanitz (1941). The correlation appears to be of decreasing availability of solar radiation with increasing melanism. This appears to be the situation with *N. defodiens* as well as with *N. investigator, N. guttula*, and, to a lesser extent, *N. vespilloides*.

Although *N. investigator* and *N. defodiens* are sympatric in many areas along the west coast, the latter is melanistic in areas where the former is not. This is due to different flight activities of the two species. (See also the discussion under Geographic variation of *N. investigator*.)

### *Nicrophorus guttula* Motschulsky

Figs. 36, 65–69, 95; Map 15

*Necrophorus guttula* Motschulsky, 1845:53.
*Necrophorus hecate* Bland, 1865:382.
*Nicrophorus guttula punctostriatus* Pierce, 1949:66.
*Nicrophorus hecate immaculosus* Hatch, 1957:15.

**Diagnosis of adult.** Pronotum strongly cordate, with narrow lateral and wide basal margins (as in Fig. 42). Antennal club either orange or with the basal segment black and the apical three segments orange. Anterior face of procoxa with long hairs on basal half. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibia straight. Elytron with pattern variable (Figs. 65–69). Moderately sized, 14–20 mm long.

*N. guttula* and *N. hecate* have long been considered separate species or subspecies based on different color patterns of elytra and antennae. Recent study (Anderson and Peck, unpublished) demonstrates that intermediates and sympatry exist and that color variations are probably locally adaptive. In view of this, we agree with Peck and Miller (1982) that the two forms are conspecific.

Map 15. Collection localities for *Nicrophorus guttula* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire, and with lateral margins truncate laterally (Fig. 95); 10th abdominal segment with base unsclerotized ventrally (as in Fig. 91). Middorsal spines of third abdominal segment three times length of lateral spines. Urogomphus with suture at base incomplete at middle.

**Distribution.** In Canada, this species is found in southern areas of British Columbia, Alberta, and Saskatchewan. It is widely distributed in the western United States.

**Natural history.** This species is an inhabitant of dry forests, prairies, and deserts. Adults are diurnal and have been collected at human and coyote dung as well as at carrion. Specimen data indicate adult activity from May through September. Overwintering probably occurs in the adult stage.

**Geographic variation.** Adults of this species exhibit extreme variation in elytral color pattern and in color of antennal club (Figs. 65–69; Hatch 1957). Forms occurring in Canada are mainly of the maculated type (Fig. 66), but in southwestern coastal areas of the United States melanic forms occur (Figs. 67–69). These melanics contrast with increasingly maculated forms (Fig. 65) in inland desert areas, with an apparent correlation between the climatic conditions of the locality and color pattern being evident (Anderson and Peck, unpublished data).

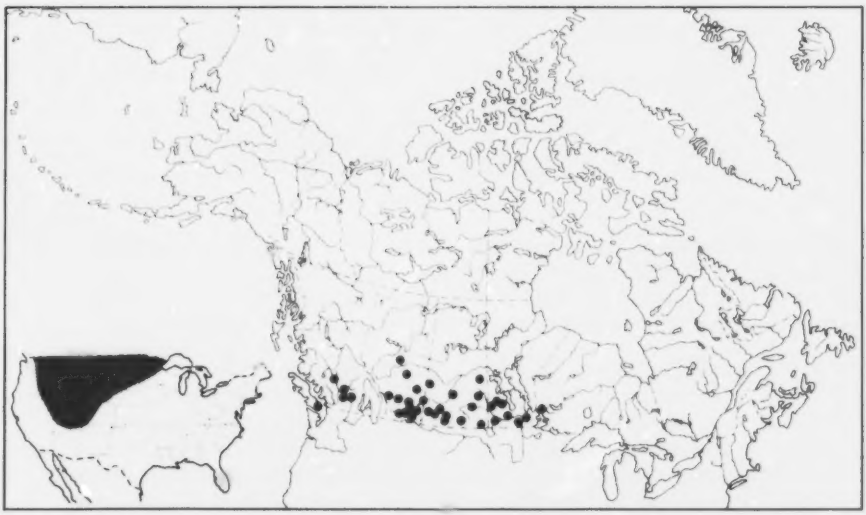
### *Nicrophorus hybridus* Hatch & Angell

Figs. 37, 41, 63; Map 16

*Necrophorus hybridus* Hatch and Angell, 1925:216.

**Diagnosis of adult.** Pronotum subquadrate, with wide lateral and basal margins (Fig. 41). Antennal club with apical three segments orange, basal segment black. Metasternum with pubescence dense, yellow, but with a bald spot behind each mesocoxa (as in Fig. 5); metepimeron glabrous. Hind tibia straight. Elytron with pattern as in Fig. 63. Moderately sized, 15–20 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base sclerotized ventrally (as in Fig. 90). Lateral spines of tergites of abdominal segments 1–3 slightly longer than, or equal to, length of middorsal spines; middorsal spines of tergites of abdominal segments 4–8 at least twice as long as lateral spines; lateral spines of tergites of abdominal segments 1–8 twice diameter of spiracle on segments 6–8; lateral spines of tergite of ninth abdominal segment large, with distance to base of urogomphus from base of lateral spine equal to length of lateral spine. Urogomphus with suture at base complete.



Map 16. Collection localities for *Nicrophorus hybridus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution.** In Canada, this species occurs in the southern areas of the Prairie Provinces, west into western British Columbia. It is also widely distributed in the north central United States.

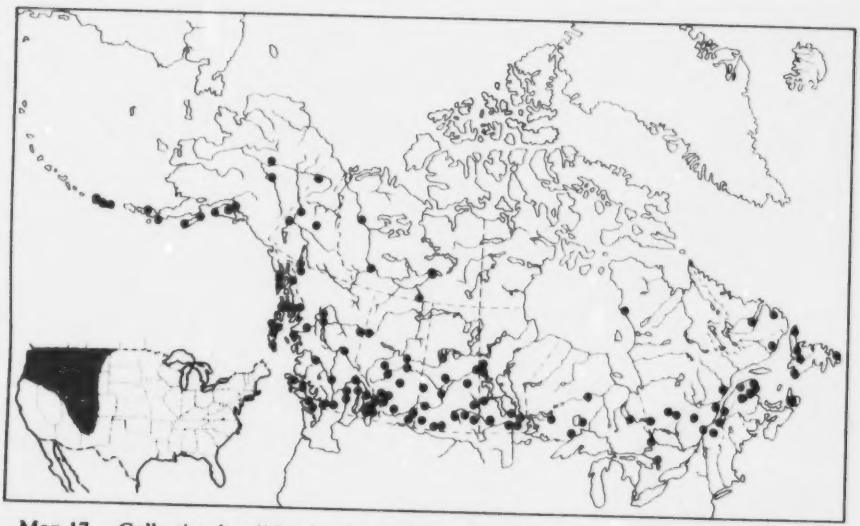
**Natural history.** *N. hybridus* is an inhabitant of prairies and dry inland valleys of the coastal provinces and states. Adults are reproductively active in summer. As in *N. tomentosus* and *N. investigator*, overwintering occurs in the prepupal stage. Adults appear to be primarily diurnal, if not exclusively so.

**Geographic variation.** None noted.

### *Nicrophorus investigator* Zetterstedt

Figs. 38, 40, 57–62, 92; Map 17

*Necrophorus investigator* Zetterstedt, 1824:154.
*Necrophorus maritimus* Escholtz *in* Guérin-Méneville, 1835:Pl. 17, Fig. 12.
*Necrophorus melsheimeri* Kirby, 1837:97.
*Necrophorus particeps* Fischer von Waldheim, 1844:139.
*Necrophorus aleuticus* Gistel, 1848:190.
*Necrophorus pollinctor* Mannerheim, 1853:169.
*Necrophorus infodiens* Mannerheim, 1853:170.
*Necrophorus confossor* LeConte, 1854:20.



Map 17. Collection localities for *Nicrophorus investigator* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of adult.** Pronotum quadrate, with wide lateral and basal margins (Fig. 40). Antennal club with apical three segments orange, basal segment black. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibia straight. Elytron with pattern variable (Figs. 57–62). Moderately sized, 13–18 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base and apex sclerotized ventrally (Fig. 92). Lateral spines of tergites of abdominal segments 3–8 approximately one-half length of middorsal spines; lateral spines of tergite of ninth abdominal segment large, with distance to base of urogomphus from base of lateral spine equal to length of lateral spine. Urogomphus with suture at base complete.

**Distribution.** This species is widely distributed throughout Canada and Alaska, though in Eastern Canada it is found primarily in northern areas. It is also widely distributed in the eastern and western United States and most of the Palearctic region.

**Natural history.** Virtually nothing has been published on the natural history of this species in North America, but work has been done on the species in Japan (Katakura and Fukuda 1975) and in Europe (Mroczkowski 1949; Pukowski 1933). These studies showed that adults first appear in mid-June through early July and are reproductively active at this time. The subsequent brood overwinters in the prepupal stage. Specimen data indicate a similar pattern of development in North America. The low level of sympatry between this species and others in North America that possess a similar developmental pattern (i.e., *N. tomentosus* and *N. hybridus*) may be indicative of competitive exclusion.

Adults are both nocturnal and diurnal in flight habits, depending on local environmental conditions (Katakura and Fukuda 1975).

**Geographic variation.** Variation in elytral pattern of adults of this species is extensive, with darker forms (Figs. 59–62) occurring on the northwest coast of North America. This melanism appears to be correlated with cooler and wetter conditions typical of these areas. Fogs are extensive in the Queen Charlotte Islands, in coastal and insular Alaska, and in the Aleutian Islands, all of which are areas where darker patterns predominate. In southern coastal areas, only typically maculated forms occur (Figs. 57, 58).

A more detailed study of the distribution and cause of melanism in North American *Nicrophorus* is in preparation by us.

## *Nicrophorus marginatus* Fabricius

Figs. 42, 70, 91, 96; Map 18

*Necrophorus marginatus* Fabricius, 1801:334.
*Necrophorus requiescator* Gistel, 1848:190.
*Necrophorus montezumae* Matthews, 1888:92.
*Necrophorus marginatus cordiger* Portevin, 1924:84.
*Nicrophorus guttula labreae* Pierce, 1949:63.
*Nicrophorus mckittricki* Pierce, 1949:66.
*Nicrophorus obtusiscutellum* Pierce, 1949:67.
*Nicrophorus investigator latifrons* Pierce, 1949:67.

**Diagnosis of adult.** Pronotum strongly cordate, with narrow lateral margins, and with wide basal margin (Fig. 42). Antennal club orange. Anterior face of procoxa with short hairs on basal half. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibia slightly curved. Elytron with pattern as in Fig. 70. Moderately sized, 15–22 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite fragmented (Fig. 96); 10th abdominal segment with base unsclerotized ventrally (Fig. 91). Urogomphus with suture at base incomplete at middle.

Map 18. Collection localities for *Nicrophorus marginatus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution**. In Canada, this species is found in extreme southern Ontario and Quebec, as well as in southern areas of Manitoba west to British Columbia. It is widely distributed in the United States, ranging south into northern Mexico.

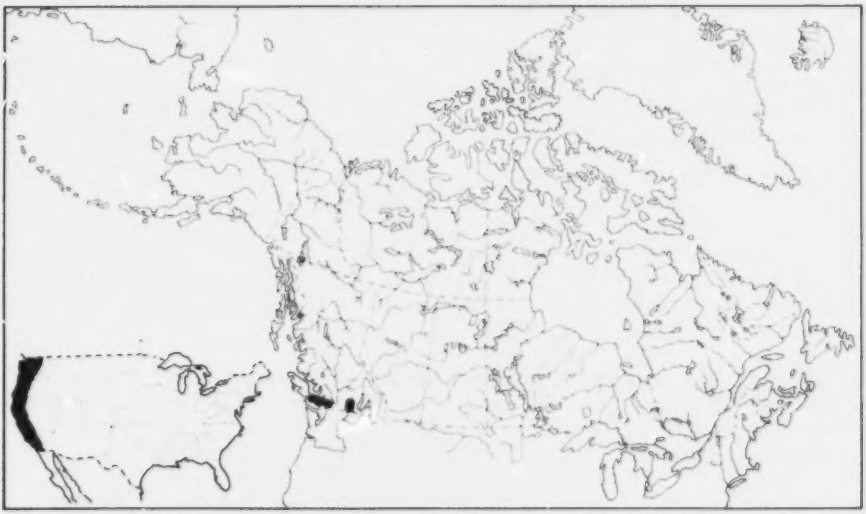
**Natural history**. *Nicrophorus marginatus* adults are first active in early May in Ontario (Anderson 1982*a*). Reproduction occurs throughout May and June with teneral adults appearing in July and August. Overwintering is in the adult stage.

In Eastern Canada, it is the only species found exclusively in open fields and meadows and may have only recently spread east from western prairie habitats as man provided cleared routes for dispersal (see Lindroth 1971 for a discussion of similar patterns in the Carabidae). It has not been determined whether adults are nocturnal or diurnal.

**Geographic variation**. In arid areas of the southwestern United States, adult specimens with anterior and posterior orange maculations fused may be found.

### *Nicrophorus nigrita* Mannerheim

Map 19



Map 19. Collection localities for *Nicrophorus nigrita* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

*Necrophorus nigrita* Mannerheim, 1843:251.
*Necrophorus ruficornis* Motschulsky, 1869:352.
*Nicrophorus investigator alpha* Pierce, 1949:67.

**Diagnosis of adult.** Pronotum quadrate, with wide lateral and basal margins (as in Fig. 40). Antennal club with apical three segments orange, basal segment black. Metasternal pubescence dense, brown; metepimeron glabrous. Hind tibia straight. Elytron entirely black. Small, 13–18 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base and apex sclerotized ventrally (as in Fig. 92). Lateral spines of tergites of seventh and eighth abdominal segments approximately one-half length of middorsal spines; lateral spines of tergite of ninth abdominal segment small, with distance from base of lateral spine to base of urogomphus equal to twice length of lateral spine. Urogomphus with suture at base complete.

**Distribution.** In Canada, this species is found rarely in southwestern British Columbia and Vancouver Island. It is widely distributed in the coastal areas of Washington, Oregon, and California.

**Natural history.** *N. nigrita* seems to be found in coastal forests. Specimen data from California indicate that adults are primarily active in the cooler and wetter months of September through May.

**Geographic variation.** None noted.

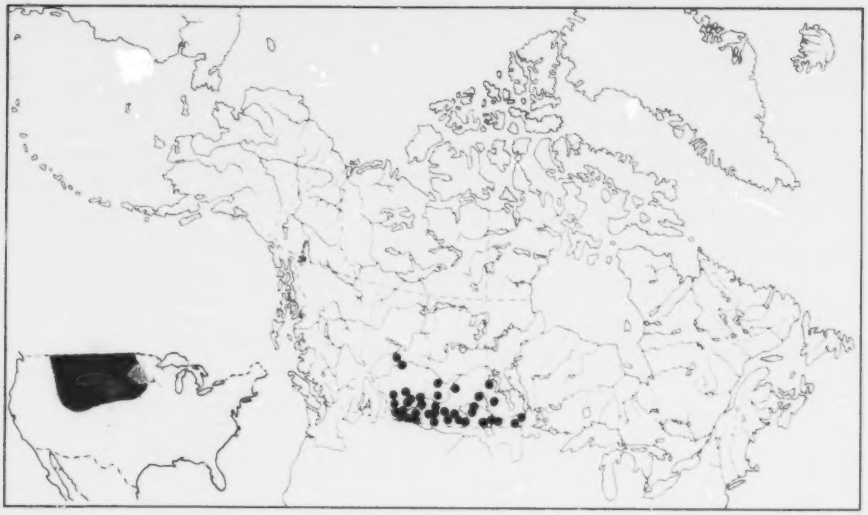
### *Nicrophorus obscurus* Kirby

Figs. 35, 71, 72, 89, 94, 97; Map 20

*Necrophorus obscurus* Kirby, 1837:57.

**Diagnosis of adult.** Pronotum strongly cordate, with narrow lateral margins and wide basal margin (as in Fig. 42). Antennal club with apical three segments orange, basal segment black; penultimate segment with outer edge deeply emarginate (Fig. 35). Anterior face of procoxa with long hairs on basal half. Metasternum and metepimeron with pubescence dense, yellow. Hind tibia slightly curved. Elytron with pattern as in Figs. 72, 73. Moderately sized, 15–25 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (Fig. 97). Ninth abdominal segment with sternite entire, and with lateral margins truncate laterally (Fig. 94); 10th abdominal segment with base unsclerotized ventrally (as in Fig. 91). Lateral and middorsal spines of tergite of third abdominal segment equal in length. Urogomphus with suture at base incomplete at middle.



Map 20. Collection localities for *Nicrophorus obscurus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Distribution**. In Canada, this species is found in southern Alberta, Saskatchewan, and Manitoba. It is also widely distributed in the north central United States.

**Natural history**. This is an inhabitant of prairies, and adult *N. obscurus* seem to be active from May to June. Adults are diurnal and have been collected at human dung and carrion. No additional information on its natural history is available.

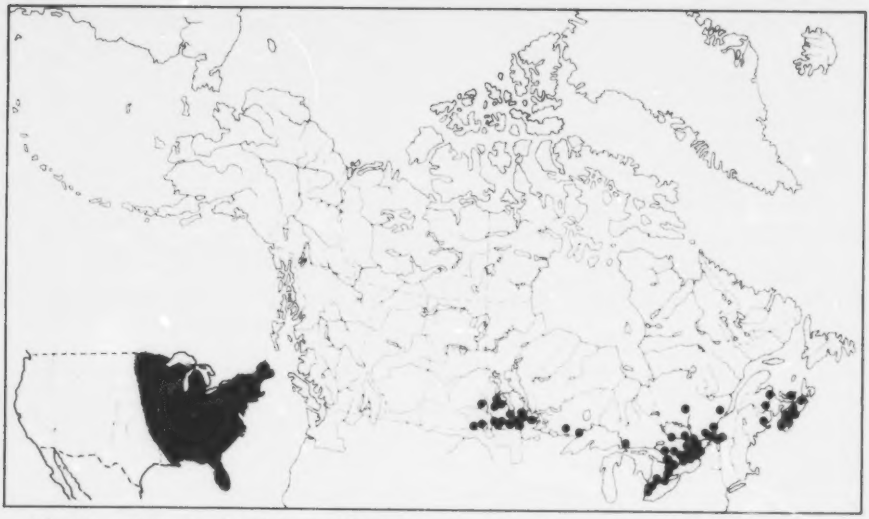
**Geographic variation**. Some specimens have the elytral maculations reduced (Fig. 72), but there appears to be no correlation with geographic locality.

### *Nicrophorus orbicollis* Say

Figs. 21, 39, 44, 45; Map 21

*Necrophorus orbicollis* Say, 1825:177.
*Necrophorus hallii* Kirby, 1837:98.
*Necrophorus quadrisignatus* Laporte, 1840:1.

**Diagnosis of adult**. Pronotum orbicular, with wide lateral and basal margins (Fig. 39). Antennal club with apical three segments orange, basal segment black. Metasternal pubescence dense, brown; metepimeron with few



Map 21. Collection localities for *Nicrophorus orbicollis* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

brown hairs. Hind tibia straight. Dorsal surface of elytron with long hairs over entire surface. Elytron with pattern as in Fig. 45. Moderately sized, 15–22 mm long.

**Diagnosis of larva**. Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base sclerotized ventrally (as in Fig. 90). Lateral spines of tergites of abdominal segments 1–3 slightly longer than, or equal to, length of middorsal spines; middorsal spines of tergites of abdominal segments 4–8 at least twice as long as lateral spines; lateral spines of tergites of abdominal segments 1–8 twice diameter of spiracle on segments 6–8; lateral spines of tergite of ninth abdominal segment minute, with distance to base of urogomphus from base of lateral spine four times length of lateral spine. Urogomphus with suture at base complete.

**Distribution**. In Canada, this species is found from Nova Scotia and New Brunswick, west to southeastern Saskatchewan. It is widely distributed in the eastern United States, west to Texas, Oklahoma, and Nebraska.

**Natural history**. Adults of *N. orbicollis* are active early in the spring, with the first adults appearing during the latter part of May in Ontario (Anderson 1982*a*), New York (Pirone 1974), and New Jersey (Shubeck 1976). Reproduction occurs at this time with teneral adults appearing in late July and early August. Overwintering takes place in the adult stage.

The species is found in both open and forested habitats but more commonly in the latter. Adults are nocturnal (Shubeck 1971), and are often caught at lights.

**Geographic variation.** None noted.

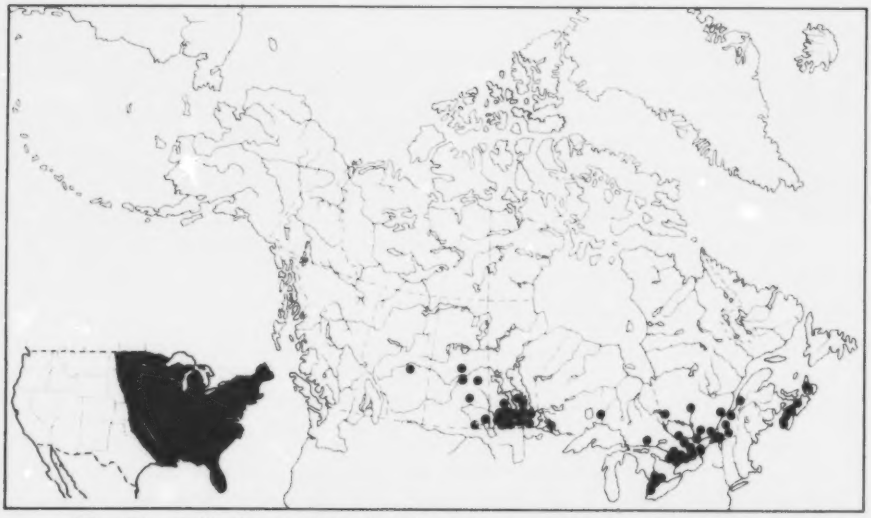
### *Nicrophorus pustulatus* Herschel

Fig. 46; Map 22

*Necrophorus pustulatus* Herschel, 1807:271.
*Necrophorus bicolon* Newman, 1838:385.
*Necrophorus tardus* Mannerheim, 1853:170.
*Necrophorus marginatus fasciatus* Portevin, 1924:86.
*Necrophorus marginatus unicolor* Portevin, 1924:86.

**Diagnosis of adult.** Pronotum transverse, subquadrate, with basal and lateral margins wide (as in Fig. 41). Antennal club with apical three segments orange, basal segment black. Metasternal pubescence sparse, yellow brown; metepimeron glabrous. Hind tibia straight. Elytron with pattern as in Fig. 46. Moderately sized, 15–20 mm long.

**Distribution.** In Canada, this species is found from Nova Scotia and New Brunswick, west to Alberta. It is also widely distributed in the eastern United States.



Map 22. Collection localities for *Nicrophorus pustulatus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Natural history**. *Nicrophorus pustulatus* is generally one of the rarer species of *Nicrophorus*. In Ontario, adults first appear in late April and early May (Anderson 1982*a*). They are reproductively active at this time, with teneral adults appearing in late July and early August. Overwintering probably takes place in the adult stage. Shubeck (1969), in New Jersey, and Pirone (1974), in New York, first record adults of this species in July.

Adults of *N. pustulatus* are nocturnal, and are commonly caught at lights. The species seems to be found in most forested habitats, but this observation is based on few specimens.

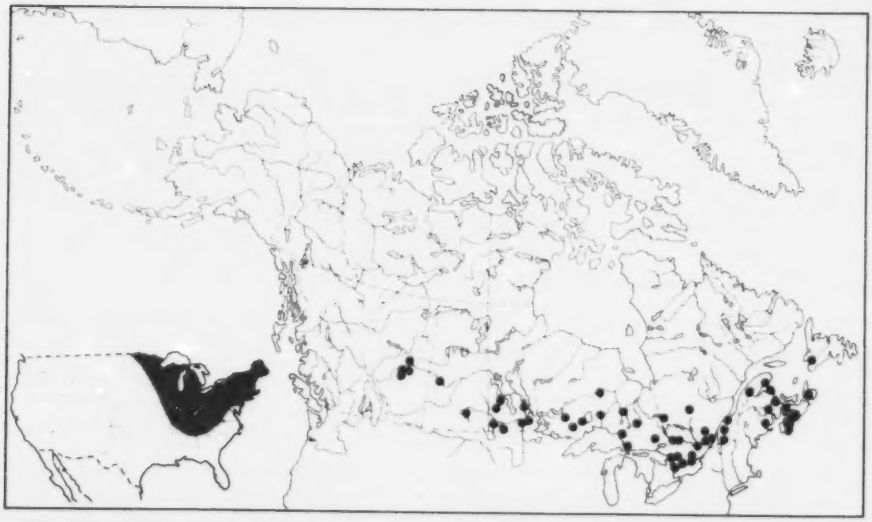
The common occurrence of adults at lights, yet their apparent rarity in pitfall traps, may indicate that the species possesses a different natural history than other *Nicrophorus*.

**Geographic variation**. None noted.

### *Nicrophorus sayi* Laporte

Frontispiece; Figs. 47, 98; Map 23

*Necrophorus sayi* Laporte, 1840:2.
*Necrophorus lunulatus* Gistel, 1848:189.
*Necrophorus lunatus* LeConte, 1853:277.
*Necrophorus luniger* Harold, 1868:104.



Map 23. Collection localities for *Nicrophorus sayi* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

**Diagnosis of adult.** Pronotum orbicular, with wide lateral and basal margins (as in Fig. 39). Antennal club with apical three segments orange, basal segment black. Metasternal pubescence sparse, yellow brown; metepimeron with few short black hairs. Hind tibia strongly curved. Elytron with pattern as in Fig. 47 and in frontispiece. Moderately sized, 15–23 mm long.

**Diagnosis of larva.** Labial palpi narrowly separated, with basal segment unsclerotized ventrally (Fig. 98). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base sclerotized ventrally (as in Fig. 90). Middorsal spines of tergites of abdominal segments 4–8 at least twice as long as lateral spines. Urogomphus with suture at base either complete or incomplete at middle.

**Distribution.** In Canada, this species is found from Newfoundland and Nova Scotia west to central Alberta. It is also widely distributed in the northeastern United States.

**Natural history.** Adults of *N. sayi* are the first adults of any species of *Nicrophorus* to become active in spring. They are often present while snow is still on the ground.

In southern Ontario (Anderson 1982*a*), the first adults appear in mid-April. Reproduction occurs at this time, with teneral adults subsequently emerging in late July through early September. Overwintering takes place in the adult stage. *N. sayi* is found in both open and forested areas, but it exhibits a greater association with the latter area. Adults are nocturnal and are often attracted to lights.

**Geographic variation.** None noted.

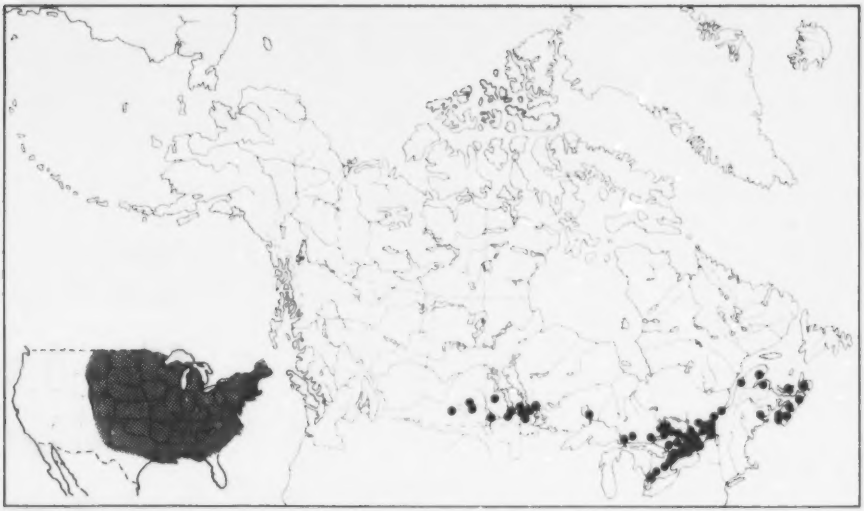
### *Nicrophorus tomentosus* Weber

Figs. 34, 64; Map 24

*Necrophorus tomentosus* Weber, 1801:47.
*Necrophorus velutinus* Fabricius, 1801:334.
*Necrophorus velutinus angustifasciatus* Portevin, 1925:170.
*Necrophorus velutinus aurigaster* Portevin, 1925:170.

**Diagnosis of adult.** Pronotum subquadrate, with wide lateral and basal margins (as in Fig. 41), covered with dense yellow pubescence. Antennal club black. Metasternum with pubescence yellow, with a bald spot behind each mesocoxa (as in Fig. 5); metepimeron with only a few yellow hairs. Hind tibia straight. Elytron with pattern as in Fig. 64. Small, 12–18 mm long.

**Diagnosis of larva.** Labial palpi widely separated, with basal segment sclerotized ventrally (as in Fig. 97). Ninth abdominal segment with sternite entire (as in Fig. 93); 10th abdominal segment with base sclerotized ventrally (as in Fig. 90). Lateral spines of tergites of abdominal segments 1–8 small,



Map 24. Collection localities for *Nicrophorus tomentosus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

not exceeding diameter of spiracle. Lateral and middorsal spines of tergite of first abdominal segment equal in length; middorsal spines of tergites of abdominal segments 2–8 at least twice as long as lateral spines. Urogomphus with suture at base complete.

**Distribution.** In Canada, this species is common from Nova Scotia and New Brunswick west to southern Saskatchewan. It is widely distributed in the eastern United States.

**Natural history.** Adults of this species are summer active, appearing first in late June and early July in Ontario (Anderson 1982*a*), New Jersey (Shubeck 1976), and New York (Pirone 1974). Unlike most other Nearctic *Nicrophorus*, adults of *N. tomentosus* do not bury the carcass. Rather, they make only a shallow pit into which the carcass sinks. This pit is then covered with leaf litter and other debris. Mature larvae, after moving into the surrounding soil, do not pupate but remain quiescent in the third instar. Winter is passed in this stage, with pupation occurring the following spring. Environmental cues that control this diapause have not yet been determined.

Adults of *N. tomentosus* are eurytopic, and are found in most habitat types. This may be due to their late season emergence, when adults of other species with which *N. tomentosus* is sympatric are not reproductively active. Adults are diurnal (Shubeck 1971) and have been recorded as mimics of adult *Bombus* (Milne and Milne 1944), which they greatly resemble when flying.

**Geographic variation.** None noted.

### *Nicrophorus vespilloides* Herbst

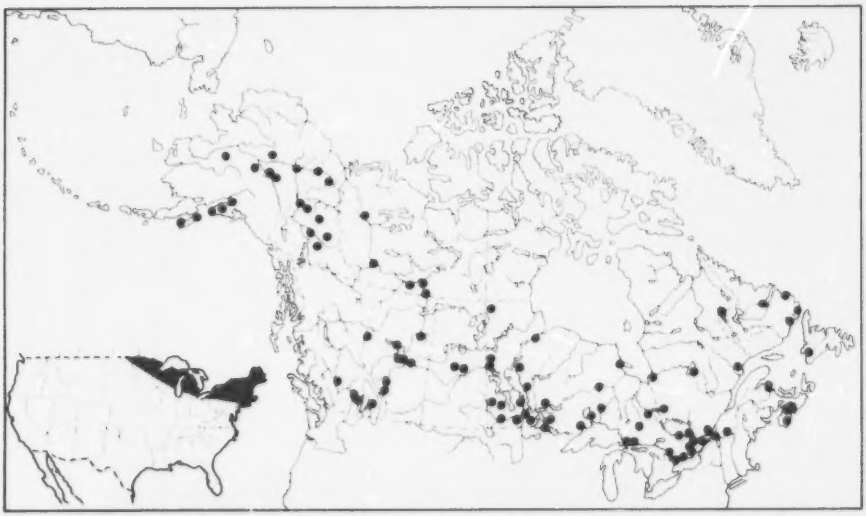
Figs. 49, 50; Map 25

*Nicrophorus vespilloides* Herbst, 1783:32.
*Necrophorus hebes* Kirby, 1837:96.
*Necrophorus pigmaeus* Kirby, 1837:98.

**Diagnosis of adult.** Pronotum quadrate, with wide lateral and basal margins (as in Fig. 40). Antenna with club entirely black; upper and lower surfaces of ninth and 10th antennal segments with dense patch of white hairs arranged in a "figure eight" pattern. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibia straight. Elytral pattern variable (Figs. 49, 50). Small, 12–16 mm long.

**Distribution.** This species is widely distributed in Canada and Alaska. In the conterminous United States, it has only been recorded from a few localities in the northeast. It is also found throughout the Palearctic region (Hatch 1928).

**Natural history.** Adults of this species are active in the spring in Ontario (Anderson 1982*a*) and probably reproduce at this time. The subsequent larval brood emerges as adults in August and September and these overwinter. This pattern conforms well with that documented by Christie (1980).



Map 25. Collection localities for *Nicrophorus vespilloides* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

*N. vespilloides* is a species of varying habitat association. In North America, it is found exclusively in swampy or boggy areas throughout the boreal forest region. In Europe, it is found exclusively in dry coniferous forests (Pukowski 1933). These habitat differences, which may be due to competitive interactions with the closely related species *N. defodiens*, are being studied by ecologists.

Adults of *N. vespilloides* do not bury the carcass; instead, they dig a shallow pit into which the carcass sinks. It is then covered with leaf litter and debris (Pukowski 1933). Adult flight habits are variable, depending on environmental conditions (Katakura and Fukuda 1975).

**Geographic variation.** In some coastal areas in northwestern Alaska and in insular Alaska, including the Aleutian Islands, there is a reduction of maculations from the typical elytral pattern. This reduction also results in a disjunction of the humeral orange spot from the rest of the orange pattern of the elytral epipleuron (Fig. 49).

## Agyrtidae

Members of the Agyrtidae are small to medium-sized, brownish beetles, 5–13 mm long, and are often associated with decaying organic material. They have traditionally been considered as silphids, but recent study (Lawrence and Newton 1982) has shown them to possess many characters allying them with the Leiodidae and not with the Silphidae. They are not known by any common name and are generally unfamiliar to most people.

The North American forms have been revised by Horn (1880) and subsequently reviewed by Hatch (1957), Miller and Peck (1979), and Peck (in press). An extensive revision is currently in progress (Newton, unpublished). Hatch (1927*a*) presents keys to genera and the species of *Necrophilus*. Van Dyke (1928) and Peck (1974) have revised the North American species of *Apteroloma* and *Agyrtes*, respectively.

Immature stages are, for the most part, undescribed. However, the recent publication by Lawrence (1982) allows for a brief diagnosis of larvae of the family.

At present we recognize 11 species in 6 genera in North America, north of Mexico, 8 of which have distributions extending into Canada and Alaska. All except one species are found in western North America.

## Natural history

What little is known of the biology of these beetles indicates that adults are scavengers of decaying organic material. Habitat associations vary, but

most species are found in wet habitats, particularly along margins of mountain streams, on high altitude snowfields, in leaf litter, and in association with some fungi. They seem to be cold-adapted and are primarily active in the colder months of winter, late fall, and early spring. Larval habits are not known, but are probably similar to those of the adults.

The group is of little economic importance.

## Methods of collecting specimens

In contrast to silphids, agyrtids are rarely collected and are often difficult to find. Adults of some species, especially members of *Necrophilus*, will come to carrion-baited traps. However, most other members of the family are rarely trapped, but are usually hand-collected. Sifting fungi or subcortical material occasionally yields specimens of *Agyrtes* and *Ipelates*. Members of *Apteroloma* and *Pteroloma* are found among gravel and moss at the banks of mountain streams, in washed up river or beach debris, and, in the case of *Apteroloma*, on high altitude snowfields. Further information on habits is given in the text.

Larvae are poorly known and no reliable method is known by which they can be collected. We expect that extensive sifting of leaf litter and streamside debris will eventually produce specimens.

## Adult anatomy

A general anatomical characterization of the family is presented elsewhere in the text. In order to facilitate the understanding of structural terms and use of keys in this book, however, a brief illustrated discussion of agyrtid anatomy is provided here. It is by no means complete and is intended solely as an aid in recognizing the states of taxonomically important characters.

**Antennae:** In agyrtids, antennae may be either filiform, as in *Lyrosoma*, or gradually clavate to varying degrees, as in the other genera. In all genera, except *Pteroloma* and *Apteroloma*, the antennae have the preapical two, or more, segments grooved around the apex (Fig. 104). A dense concentration of setae is found in this groove.

**Clypeus:** The clypeus can be of two basic shapes in agyrtids: pentagonal, as in *Necrophilus, Ipelates*, and *Lyrosoma* (Figs. 100, 103), or rectangular, as in *Pteroloma, Apteroloma*, and *Agrytes* (Figs. 99, 101, 102).

**Mandibles:** The presence or absence of preapical mandibular teeth is important in recognizing certain genera. They are present in members of *Pteroloma* and *Apteroloma* (Figs. 101, 102) and are lacking in other genera.

**Maxillae:** In agyrtids, members of the genus *Agyrtes* can be easily recognized by having the last segment of the maxillary palpus swollen (Fig. 99). In other genera the last segment is cylindrical (Fig. 100).

**Pronotum:** As with silphids, the shape of the pronotum is an important taxonomic character. In agyrtids, members of *Lyrosoma* have a cordate pronotum (Fig. 108). The pronota of other genera vary in shape but are generally subquadrate to quadrate. In members of *Pteroloma*, the pronotum possesses rounded fovea at the middle of the base and at the posterior corners (Fig. 109).

**Elytron:** In agyrtids, the elytra of most genera are nine-striate, but in members of *Agyrtes* the elytra are 10-striate. Elytra of all family members are always uniformly brown, cover the entire abdomen, and often possess distinct microsculpture. Members of *Agyrtes* can be recognized by the depressed epipleural ridge, just posterior to the elytral shoulder (Fig. 110). This ridge is evenly rounded in all other Agyrtidae (Fig. 111). Presence or absence of punctation on the elytral epipleuron is also important for recognizing species of *Apteroloma*.

Important for recognizing the different species in *Apteroloma* and *Necrophilus* is the shape of the apices of the elytra. They can be either truncate (Fig. 115) or rounded (Fig. 114) in *Necrophilus*, and toothed (Fig. 112) or not (Fig. 113) in *Apteroloma*. Deepness of punctures is also an important character for separating the species of *Necrophilus*.

**Metathorax:** Position of the metacoxae in agyrtids separates the genera *Lyrosoma* and *Agyrtes* from the others. They are narrowly separated in these two genera and contiguous in the rest. In some family members, membranous wings are absent and such individuals are flightless.

**Genitalia:** As in silphids, examination of genitalia is not normally required for accurate species identifications.

## Family Agyrtidae

Adult members of the family Agyrtidae can be recognized by their generally small to medium size; brownish, glabrous, nine- or 10-striate elytra, which cover the entire abdomen; and antennae filiform to gradually clavate, never with eighth segment narrower than seventh and ninth segments. Members of *Apteroloma* and *Pteroloma* are similar to carabids in general appearance. A more detailed description of the family can be found in Lawrence (1982).

Larvae can be recognized by the mandibles possessing a large and tuberculate molar part; maxilla with distinct galea and lacinia; labium with strongly bilobed ligula; six ocelli on each side of head; and urogomphi two-segmented, often with a multiannulate apical segment (Lawrence 1982).

## Key to genera of adult Agyrtidae of North America

1. Mandible with 1 or 2 large preapical teeth on inner margin (Figs. 101, 102). Antenna with all segments lacking apical grooves (Fig. 105) ..... 5
Mandible lacking preapical teeth (Fig. 103). Antenna with 2, or more, preapical segments each with an apical groove containing a dense concentration of setae (Fig. 104) ..... 2

2(1). Elytron 10-striate; dorsal ridge of elytral epipleuron depressed behind shoulder (Fig. 110). Maxilla with last segment of palpus swollen (Fig. 99) ... ..... ***Agyrtes*** **Frölich** (p. 77)
Elytron 9-striate; dorsal ridge of elytral epipleuron evenly rounded (Fig. 111). Maxilla with last segment of palpus not swollen, cylindrical (Fig. 100) ..... 3

3(2). Body form elongate. Pronotum cordate, widest in anterior one-half, not as wide as elytra at base (Fig. 108) ... ***Lyrosoma*** **Mannerheim** (p. 83)
Body form ovoid. Pronotum not cordate, almost as wide as elytra at base ..... 4

4(3). Length greater than 8 mm. Pronotum with lateral margins widely explanate ..... ***Necrophilus*** **Latreille** (p. 84)
Length less than 8 mm. Pronotum with lateral margins narrowly explanate ..... ***Ipelates*** **Reitter** (p. 82)

5(1). Pronotum with rounded fovea at middle of base and in posterior corners (Fig. 109) ..... ***Pteroloma*** **Gyllenhal** (p. 87)
Pronotum lacking fovea (Figs. 106, 107) ... ***Apteroloma*** **Hatch** (p. 78)

## Tableau de détermination des genres d'Agyrtidae (adultes) d'Amérique du Nord

1. Mandibule avec 1 ou 2 grandes dents préapicales sur la marge interne (fig. 101 et 102). Antenne avec tous les articles sans sillon apical (fig. 105) ..... 5
Mandibule sans dent préapicale (fig. 103). Antenne avec au moins 2 articles préapicaux portant chacun un sillon apical renfermant une forte concentration de soies (fig. 104) ..... 2

2(1). Élytre avec 10 stries; carène dorsale de l'épipleure de l'élytre abaissée en arrière de l'épaule (fig. 110). Dernier article du palpe maxillaire enflé (fig. 99) ..... ***Agyrtes*** **Frölich** (p. 77)
Élytre avec 9 stries; carène dorsale de l'épipleure de l'élytre régulièrement arrondie (fig. 111). Dernier article du palpe maxillaire non enflé et cylindrique (fig. 100) ..... 3

3(2). Forme du corps allongée. Pronotum cordiforme, sa largeur maximale dans la moitié antérieure, plus étroit que les élytres à la base (fig. 108) .... ..... ***Lyrosoma*** **Mannerheim** (p. 83)
Forme du corps ovoïde. Pronotum non cordiforme, presque aussi large que les élytres à la base ..... 4

4(3). Longueur du corps supérieure à 8 mm. Pronotum avec les marges latérales très élargies et aplanies ..... ***Necrophilus*** **Latreille** (p. 84)
Longueur du corps inférieure à 8 mm. Pronotum avec les marges latérales étroitement élargies et aplanies ..... ***Ipelates*** **Reitter** (p. 82)

5(1). Pronotum avec une fovéole ronde au milieu de la base et aux coins postérieurs (fig. 109) ..... ***Pteroloma*** **Gyllenhal** (p. 87)
Pronotum sans fovéole (fig. 106 et 107) .... ***Apteroloma*** **Hatch** (p. 78)

## Genus *Agyrtes* Frölich

*Agyrtes* Frölich, 1799:15; Hatch 1928:73; Hlisnikovsky 1964*a*:275; Peck 1974:501; Madge 1980:354.
*Agyrtecanus* Reitter, 1901:102.
*Lendomus* Casey, 1924:185.

There are two species of the genus *Agyrtes* in North America, one of which has a distribution extending into Canada. Adults can be recognized by the 10-striate elytra with depressed epipleural ridge (Fig. 110) and by the maxilla with palpi with the apical segment swollen (Fig. 99). Larvae are undescribed.

### Key to species of adult *Agyrtes* in North America

1. Antenna with club composed of 4 segments. Posterior angles of pronotum sharp. Elytral epipleuron glabrous .. ***A. longulus*** **(LeConte)** (p. 77)
   Antenna with club composed of 5 segments. Posterior angles of pronotum rounded. Elytral epipleuron pubescent ..... ***A. similis*** **Fall***

*Distributed in southern California

### Tableau de détermination des espèces d'*Agyrtes* (adultes) d'Amérique du Nord

1. Massue antennaire de 4 articles. Angles postérieurs du pronotum distincts. Épipleure de l'élytre glabre ..... ***A. longulus*** **(LeConte)** (p. 77)
   Massue antennaire de 5 articles. Angles postérieurs du pronotum arrondis. Épipleure de l'élytre pubescent ..... ***A. similis*** **Fall***

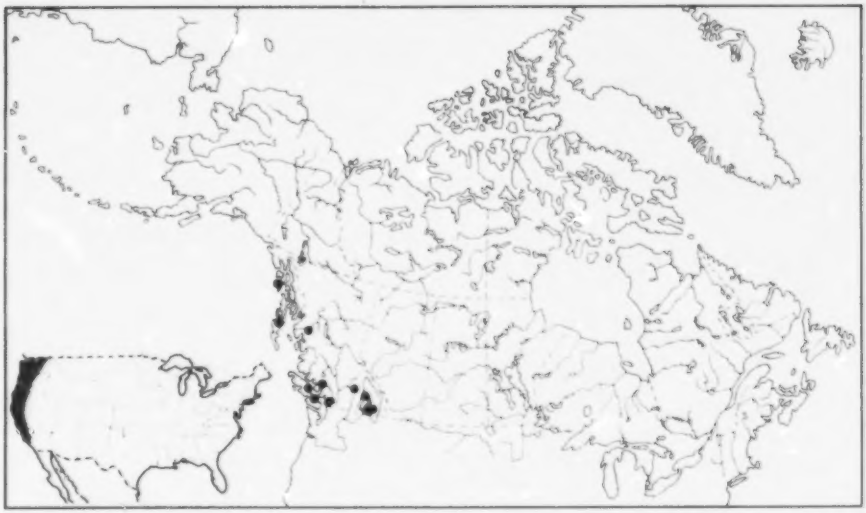
*Espèce répartie dans le sud de la Californie.

#### *Agyrtes longulus* (LeConte)

Figs. 99, 110; Map 26

*Necrophilus longulus* LeConte, 1859*c*:282.
*Lendomus politus* Casey, 1924:185.
*Agyrtes longulus*: Horn 1880:246.

**Diagnosis of adult.** Elongate, dark brown beetles. Antenna clavate, with club composed of 4 segments, short, reaching slightly beyond middle of pronotum; preapical 3 antennal segments grooved at apices (as in Fig. 104). Clypeus transversely rectangular, longer than labrum (Fig. 99).



Map 26. Collection localities for *Agyrtes longulus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

Mandibles lacking preapical teeth. Maxillae with palpi with last segment swollen, oval (Fig. 99). Pronotum slightly wider than long, as wide as elytra at base. Elytron 10-striate and with epipleural ridge depressed behind elytral shoulder (Fig. 110); intervals shiny, with no apparent microsculpture. Length 5–7 mm.

**Distribution**. This species is widely distributed in coastal areas from the Alaskan Panhandle south to southern British Columbia. In the United States, it is found from the state of Washington, south to southern California.

**Natural history**. Adults of this species have been collected on snow, on flood debris, and from under bark of living oak, Engelmann spruce, and western larch. They have also been collected in association with *Bibio* larvae (Diptera: Bibionidae). Specimen data indicate that adults are primarily active in the winter months.

**Geographic variation**. None noted.

## Genus *Apteroloma* Hatch

*Apteroloma* Hatch, 1927*b*:12; Hatch 1928:70; Madge 1980:354.

Four species of this genus are found in North America, two of which have distributions extending into Canada. Species of the genus also occur

at high elevations in Mexico. Adults can be recognized by the presence of preapical teeth on the mandibles (Fig. 102), by the ungrooved antennal segments (Fig. 105), by the contiguous hind coxae, and by the possession of an evenly rounded, smooth pronotum. Larvae are undescribed.

Adults are often confused with carabids, because they are frequently found in the same habitats and are similar in overall appearance.

## Key to species of adult *Apteroloma* in North America

1. Elytral epipleuron impunctate ..... 2
   Elytral epipleuron punctate (Fig. 111) ..... 3
2(1). Elytron with internal sutural angle bearing a distinct tooth (Fig. 112). Pronotum narrow, with base less than one and one-third times length along midline (Fig. 107) ..... ***A. caraboides*** **(Fall)** (p. 80)
   Elytron with internal sutural angle lacking a distinct tooth (Fig. 113). Pronotum broad, with base more than one and one-half times length along midline (Fig. 106) ..... ***A. tahoecum*** **(Fall)***
3(1). Posterior angles of pronotum obtusely angulate ..... ***A. arizonicum*** **(Van Dyke)****
   Posterior angles of pronotum rounded ..... ***A. tenuicorne*** **(LeConte)** (p. 81)

* Distributed in the Sierra Nevada Mountains of California and adjacent Oregon.
**Distributed in Arizona, New Mexico, and possibly west Texas.

## Tableau de détermination des espèces d'*Apteroloma* (adultes) d'Amérique du Nord

1. Épipleure de l'élytre lisse ..... 2
   Épipleure de l'élytre ponctué (fig. 111) ..... 3
2(1). Élytre avec l'angle sutural interne portant une dent distincte (fig. 112). Pronotum étroit, sa base moins d'une fois et un tiers sa longueur le long de la ligne centrale (fig. 107) ..... ***A. caraboides*** **(Fall)** (p. 80)
   Élytre avec l'angle sutural interne sans dent distincte (fig. 113). Pronotum large, sa base plus d'une fois et un tiers sa longueur le long de la ligne centrale (fig. 106) ..... ***A. tahoecum*** **(Fall)***
3(1). Angles postérieurs du pronotum obtus .... ***A. arizonicum*** **(Van Dyke)****
   Angles postérieurs du pronotum arrondis ..... ***A. tenuicorne*** **(LeConte)** (p. 81)

* Espèce répartie dans les Sierra Nevada de la Californie et les régions adjacentes de l'Orégon.

** Espèce répartie en Arizona, au Nouveau-Mexique et peut-être dans l'ouest du Texas.

### *Apteroloma caraboides* (Fall)

Figs. 102, 107, 112; Map 27

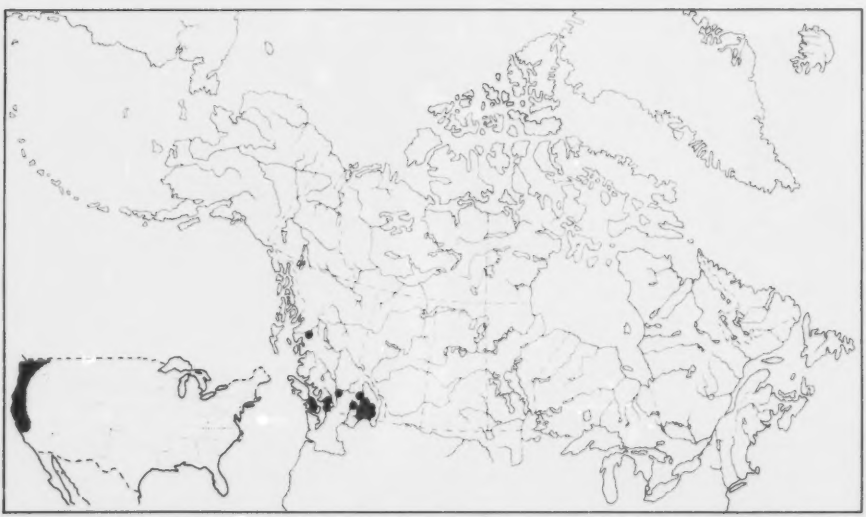
*Pteroloma caraboides* Fall, 1907:235.
*Apteroloma caraboides*: Hatch 1928:70.

**Diagnosis of adult.** Elongate, brownish beetles. Antennae gradually clavate, long, extending to anterior one-third of elytra. Clypeus transversely rectangular, slightly longer than labrum (Fig. 102). Maxillae with palpi with apical segment cylindrical. Pronotum evenly rounded, quadrate, with base less than one and one-third times length along midline (Fig. 107). Elytron 9-striate; intervals with distinct isodiametric microsculpture; sutural apices each bearing sharp tooth on inner margin (Fig. 112). Elytral epipleuron impunctate. Length 8–10 mm.

**Distribution.** This species is found from central to southern British Columbia, west of the main ridge of the Rockies. In the United States, it is found from northern Washington and Idaho, south to northern California.

**Natural history.** This species is a rare inhabitant of stream and river banks. Adult specimens have been collected among drift on beaches and in rivers. In southern localities, it is locally common on snowfields at high elevations, both nocturnally and diurnally. It is probably a scavenger in these habitats. Specimen data indicate summer activity.

**Geographic variation.** None noted.



Map 27. Collection localities for *Apteroloma caraboides* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

## *Apteroloma tenuicorne* (LeConte)

Figs. 106, 111, 113; Map 28

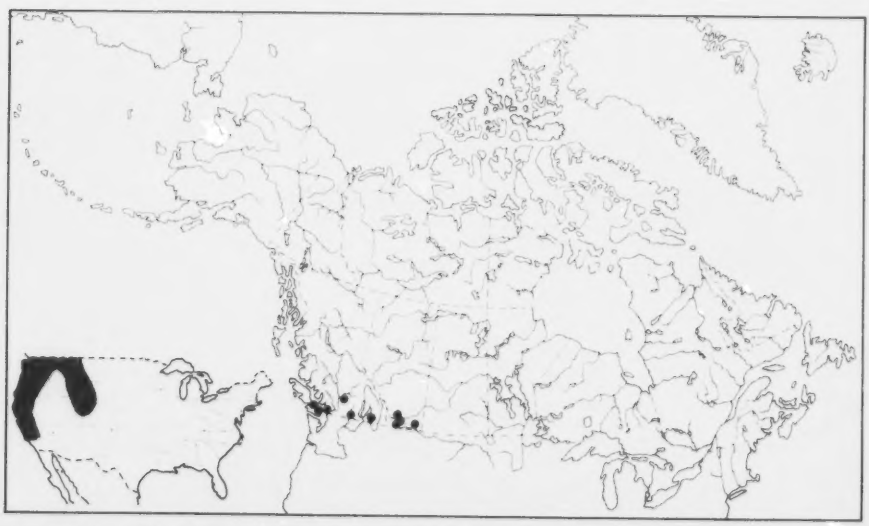
*Necrophilus tenuicornis* LeConte, 1859*b*:84.
*Apteroloma tenuicorne*: Hatch 1927*b*:12.

**Diagnosis of adult.** Elongate, brownish beetles. Antennae gradually clavate, short, extending to base of elytra or only slightly beyond. Clypeus transversely rectangular, slightly longer than labrum in length (as in Fig. 102). Maxillae with palpi with apical segment cylindrical. Pronotum evenly rounded, quadrate, with base more than one and one-half times length along midline (Fig. 106). Elytron 9-striate; intervals lacking microsculpture; sutural apices lacking tooth on inner margin (Fig. 113). Elytral epipleuron punctate (Fig. 111). Length 5–7 mm.

**Distribution.** This species is distributed from southwestern British Columbia, east to southwestern Alberta. In the United States, it is found from Washington and Idaho, south to California and Colorado.

**Natural history.** This species is a rare inhabitant of damp or wet habitats, particularly stream or river banks, lakeshores, beaches, and, nocturnally, at edges of melting snowfields (Hatch 1940; 1957). Adults have also been collected on snowbanks and along edges of large rivers in prairie habitats in spring. Some of these individuals are tenerals and it is likely that larval development takes place in nearby habitat.

**Geographic variation.** None noted.



Map 28. Collection localities for *Apteroloma tenuicorne* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

## Genus *Ipelates* Reitter

*Ipelates* Reitter, 1884:89; Hatch 1928:74; Madge 1980:355; Schawaller 1983:102.
*Pelates* Horn, 1880:244 (junior homonym, not Cuvier).
*Pelatines* Cockerell, 1906:240 (replacement name for *Pelates* Horn).

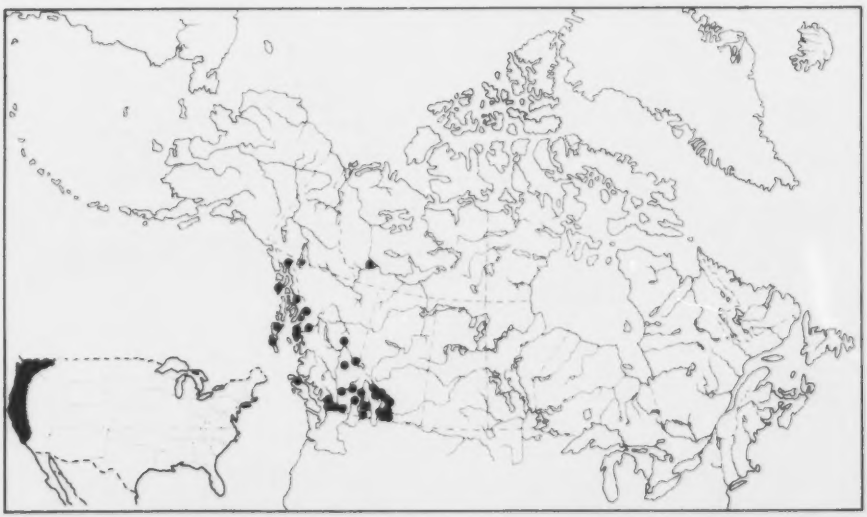
There is only one species of this genus found in North America. Adults can be recognized by the key characters, their small size, and their ovoid shape. Larvae are undescribed.

### *Ipelates latus* (Mannerheim)

Fig. 100; Map 29

*Necrophilus latus* Mannerheim, 1852:331.
*Pelates latus* Horn, 1880:244.
*Pelatines latus*: Cockerell 1906:240.
*Ipelatus latus*: Schawaller 1983:105.

**Diagnosis of adult.** Ovoid, brownish beetles. Antennae gradually clavate, reaching almost to base of pronotum, with preapical 4 segments grooved at apices (as in Fig. 104). Clypeus transversely pentagonal (Fig. 100),



Map 29. Collection localities for *Ipelates latus* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

longer than labrum. Mandibles lacking preapical teeth. Pronotum wider than long, explanate, as wide as elytra at base. Elytron 9-striate, with intervals lacking distinct microsculpture. Hind coxae contiguous. Length 4–6 mm.

**Distribution**. This species is widely distributed from British Columbia and western Alberta, north to the Alaskan Panhandle and the southwestern Northwest Territories. In the United States, it is found from Washington south to California, inland to Montana and Idaho.

**Natural history**. Adults are apparently general scavengers in leaf litter. We have most often collected them by sifting moist leaf litter or decaying mushrooms. Teneral adults seem to be most common in late July and August, indicative of adult emergence at these times. Many of these individuals are found associated with mushrooms, often around the bases of lodgepole pine and Douglas-fir. Possibly this could be a site of reproductive activity, but it could also be a site of adult feeding. Adults are also sometimes collected from under the bark of decaying trees and along the edges of streams.

**Geographic variation**. None noted.

## Genus *Lyrosoma* Mannerheim

*Lyrosoma* Mannerheim, 1853:174; Hatch 1928:71; Hlisnikovsky 1964*b*:39; Madge 1980:355.

There is only one species of the genus *Lyrosoma* found in North America. Adults are characterized by the almost filiform antennae and by the cordate pronotum (Fig. 108). Larvae are undescribed.

### *Lyrosoma opacum* Mannerheim

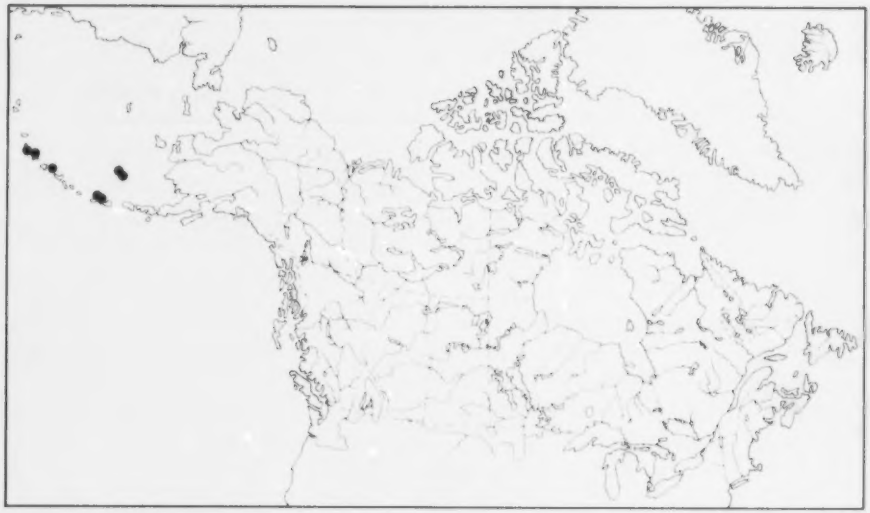
Fig. 108; Map 30

*Lyrosoma opacum* Mannerheim 1853:175.

**Diagnosis of adult**. Elongate, brownish beetles. Antennae almost filiform, long, reaching as far as anterior one-third of elytra; preapical antennal segments grooved at apices (as in Fig. 104). Clypeus transversely pentagonal, equal to labrum in length. Mandibles lacking preapical teeth. Pronotum cordate, much narrower than elytra at base (Fig. 108), not explanate. Elytron 9-striate, with intervals dull, and with distinct isodiametric microsculpture. Hind coxae narrowly separated. Metathoracic wings absent. Length 8–9 mm.

**Distribution**. This species is distributed on the western Aleutian Islands.

**Natural history**. Adults of this species have been recorded from rotting kelp and other seaweed on beaches and shore areas that are frequently inundated by high tides (Van Dyke 1921; Hatch 1927*a*). Kellogg (1914) records



Map 30. Collection localities for *Lyrosoma opacum* in Canada and Alaska.

adults from murre nests (seabirds) among broken eggs after the nests have been abandoned. It is probably a general scavenger in these habitats feeding on decaying organic material. Specimen data indicate activity in the summer months.

**Geographic variation.** None noted.

## Genus *Necrophilus* Latreille

*Necrophilus* Latreille, 1829:500; Hatch 1928:75; Madge 1980:356.
*Necrobius* Gistel, 1834:147.

There are two species of this genus found in North America, one in the east and one in the west. Adults are easily distinguished among agyrtids by the following characteristics: large size; ovoid form; clavate antennae with the preapical four segments bearing apical grooves (Fig. 104); maxillary palpi with cylindrical apical segment (as in Fig. 103); and contiguous hind coxae. North American larvae are undescribed.

## Key to species of adult *Necrophilus* in North America

1. Elytra with striae having large deep distinct punctures; intervals 2, 4, and 6 raised, convex; sutural angles truncate, each with sharp tooth at inner angle (Fig. 115). Metathoracic wings absent ..... ..... *N. pettitii* **Horn** (p. 86)

Elytra with striae having small shallow punctures; all intervals of uniform elevation; sutural angles evenly rounded (Fig. 114). Metathoracic wings present ..... *N. hydrophiloides* **Guérin-Méneville** (p. 85)

## Tableau de détermination des espèces de *Necrophilus* (adultes) d'Amérique du Nord

1. Stries des élytres avec de grands points profonds; interstries 2, 4 et 6 soulevées, convexes; angles suturaux tronqués, chacun avec une dent nette à l'angle interne (fig. 115). Ailes métathoraciques absentes ..... ..... *N. pettitii* **Horn** (p. 86)

Stries des élytres avec de petits points peu profonds; interstries uniformes; angles suturaux régulièrement arrondis (fig. 114). Ailes métathoraciques présentes ..... *N. hydrophiloides* **Guérin-Méneville** (p. 85)

### *Necrophilus hydrophiloides* Guérin-Méneville

Figs. 103, 104, 114; Map 31

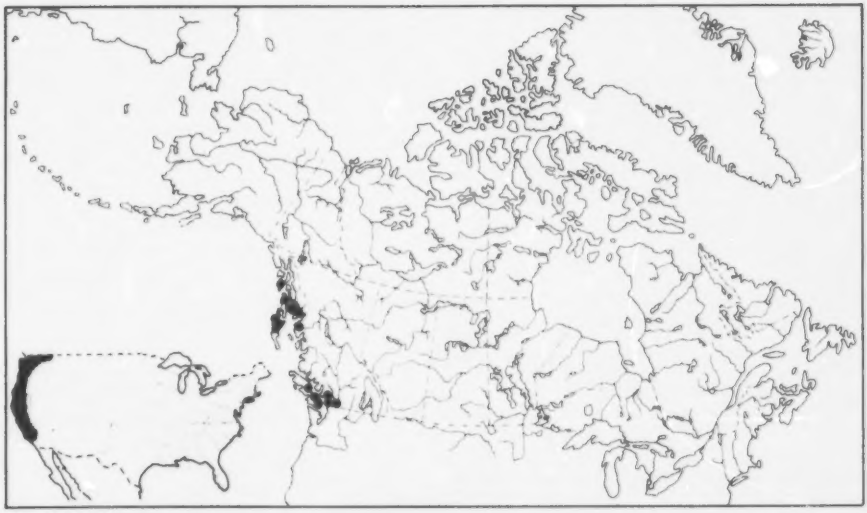
*Necrophilus hydrophiloides* Guérin-Méneville, 1835:Pl. 17, Fig. 12.

**Diagnosis of adult.** Ovoid, brownish beetles. Clypeus transversely pentagonal, longer than labrum. Pronotum explanate, as wide as elytra at base, with lateral margins not reflexed upward. Elytron 9-striate; striae with punctures small, shallow; all intervals of equal elevation; sutural apex evenly rounded (Fig. 114). Metasternum of normal length; metathoracic wings present. Length 10–13 mm.

**Distribution.** This species is found in the coastal areas of Canada and Alaska from the Alaskan Panhandle and the Queen Charlotte Islands south to southern British Columbia. In the United States, it is found from Washington and Idaho, south to southern coastal California.

**Natural history.** Adults and larvae of this species are scavengers on decaying organic material in wet coastal rainforests. Adults have been caught commonly at carrion, in garbage, and in decaying vegetable material. Specimen data indicate peak adult activity in the winter months from November to May.

**Geographic variation.** None noted.



Map 31. Collection localities for *Necrophilus hydrophiloides* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

### *Necrophilus pettitii* Horn

Fig. 115; Map 32

*Necrophilus pettitii* Horn, 1880:243.

**Diagnosis of adult.** Ovoid, brownish beetles. Clypeus transversely pentagonal, longer than labrum. Pronotum explanate, as wide as elytra at base, with lateral margins reflexed upward. Elytron 9-striate; striae with punctures large, deep, distinct; intervals 2, 4, and 6 raised; sutural apex with sharp tooth at inner angle (Fig. 115). Metasternum short; metathoracic wings absent. Length 9–12 mm.

**Distribution.** In Canada, this species is known only from the type locality in extreme southern Ontario. In the United States, it is widespread in the Appalachian states from New York, Michigan, and Illinois south to Alabama, Georgia, and northern Florida.

**Natural history.** Peck (1981) has recently summarized what is known of the natural history of this species. Adults have been recorded from carrion (Reed 1958; Peck 1981) and fungi (Pettit 1869; Blatchley 1910; Peck 1981). Reproductive activity takes place in the winter months.

**Geographic variation.** None noted.

Map 32. Collection localities for *Necrophilus pettitii* in Canada and Alaska. Inset map shows general distribution in the conterminous United States.

## Genus *Pteroloma* Gyllenhal

*Pteroloma* Gyllenhal, 1827:418; Hatch 1928:68; Madge 1980:358.
*Adolus* Fischer von Waldheim, 1828:242.
*Holocnemis* Schilling, 1829:93.

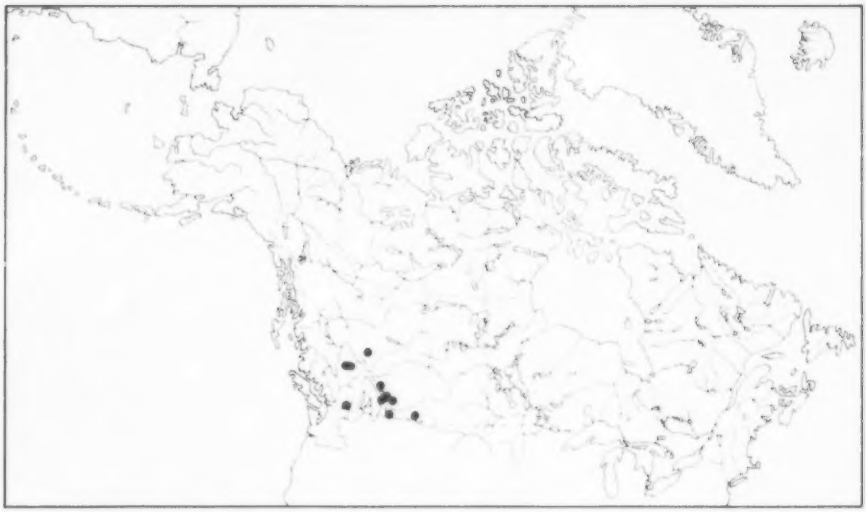
There is only a single species of this genus in North America. Adults can easily be recognized by the foveolate pronotum (Fig. 108). Larvae are undescribed.

### *Pteroloma nebrioides* Brown

Figs. 101, 105, 109; Map 33

*Pteroloma nebrioides* Brown, 1933:213.

**Diagnosis of adult.** Elongate, brownish beetles. Antennae gradually clavate, reaching to anterior one-third of elytra, with all segments lacking apical grooves (Fig. 105). Clypeus transversely rectangular, only slightly longer than labrum (Fig. 101). Mandibles with 1 or 2 large preapical teeth (Fig. 101). Maxillae with palpi with apical segment cylindrical (Fig. 101). Pronotum quadrate, not broadly explanate, with rounded fovea at middle of base and in posterior corners, not as wide as elytra at base (Fig. 109). Elytron



Map 33. Collection localities for *Pteroloma nebrioides* in Canada and Alaska.

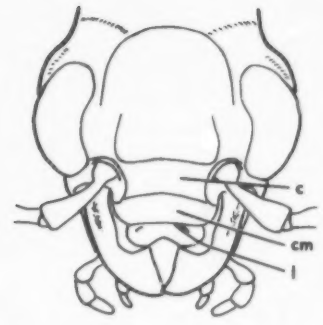
9-striate; intervals with no apparent microsculpture; epipleuron coarsely, irregularly punctate. Hind coxae contiguous. Length 5–7 mm.

**Distribution.** This species is found in the southern montane areas of eastern British Columbia and western Alberta. In the United States, it is known only from extreme northwestern Montana.

**Natural history.** Adults have been collected in moss and among rocks and gravel along the banks of shaded mountain streams that are 3–5 m wide and at elevations of between 1000 and 1800 m. Although often found among the rocks, many specimens were collected from mossy banks that were overhanging the water. This may be an area where food, presumably decaying organic material carried by the stream, is deposited. Adults may therefore be attracted to these areas to feed.

Adults are primarily active in late spring and early summer. At this time, mating and oviposition take place. Based on observations of two females, two large yellowish eggs (1.5 mm in diameter) are laid by a female in damp moss. Larvae were not noted, but they probably feed as scavengers in the same habitats as the adults.

**Geographic variation.** None noted.

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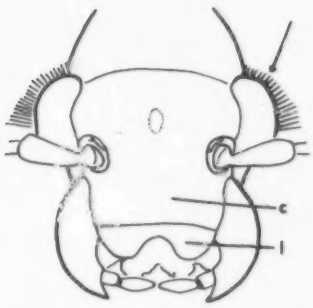


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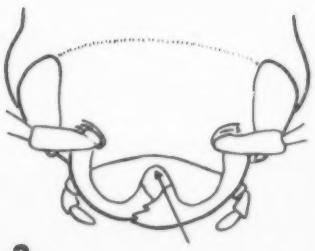

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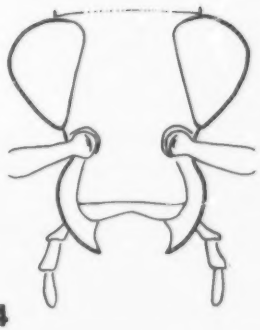

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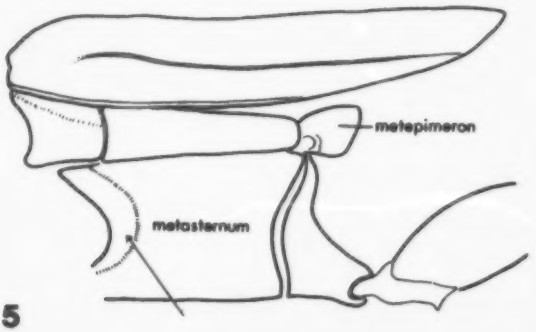


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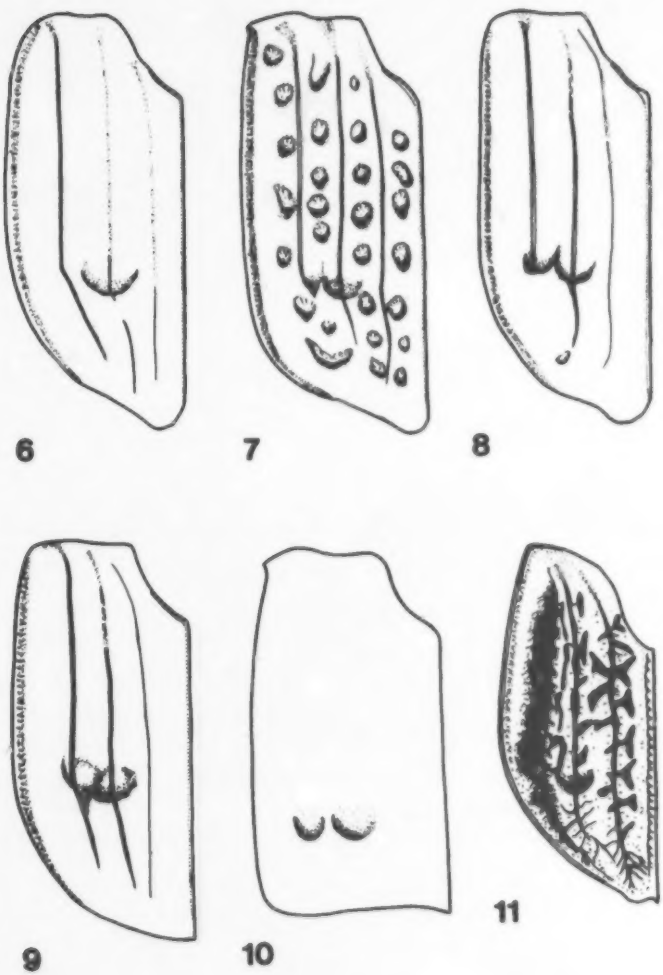
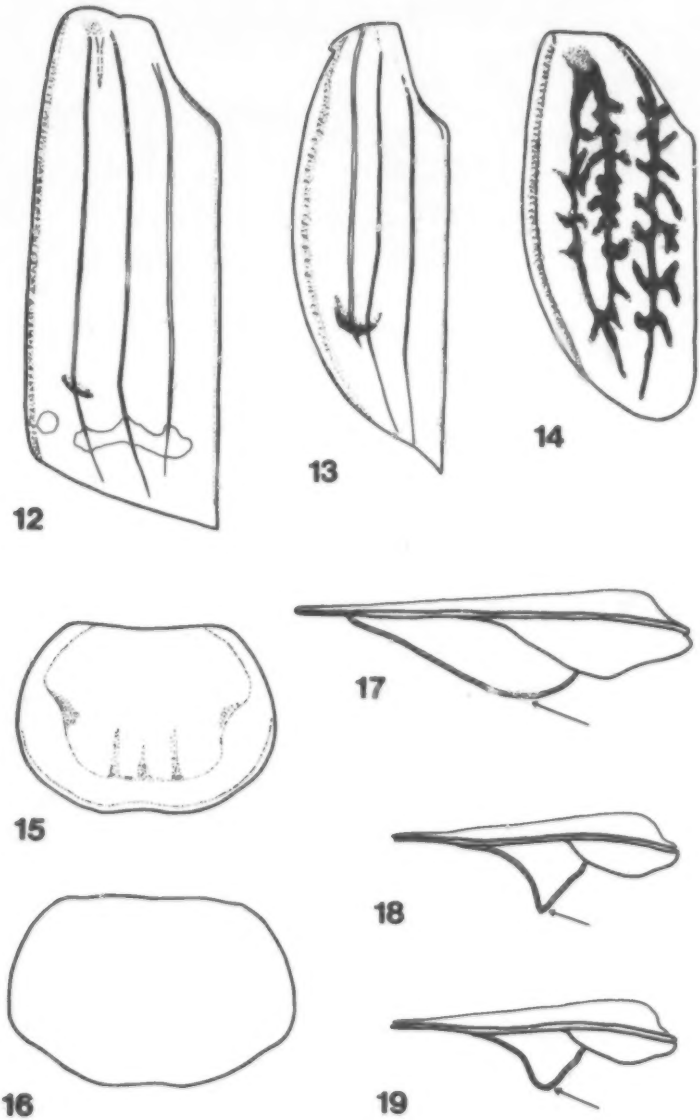
Figs. 1–4. Heads of adult Silphidae (dorsal view: *c*, clypeus; *cm*, clypeal membrane; *l*, labrum). 1, *Nicrophorus defodiens*; 2, *Necrophila americana*; 3, *Aclypea bituberosa*; 4, *Necrodes surinamensis*.

Fig. 5. Elytron and metathorax of *Nicrophorus*.



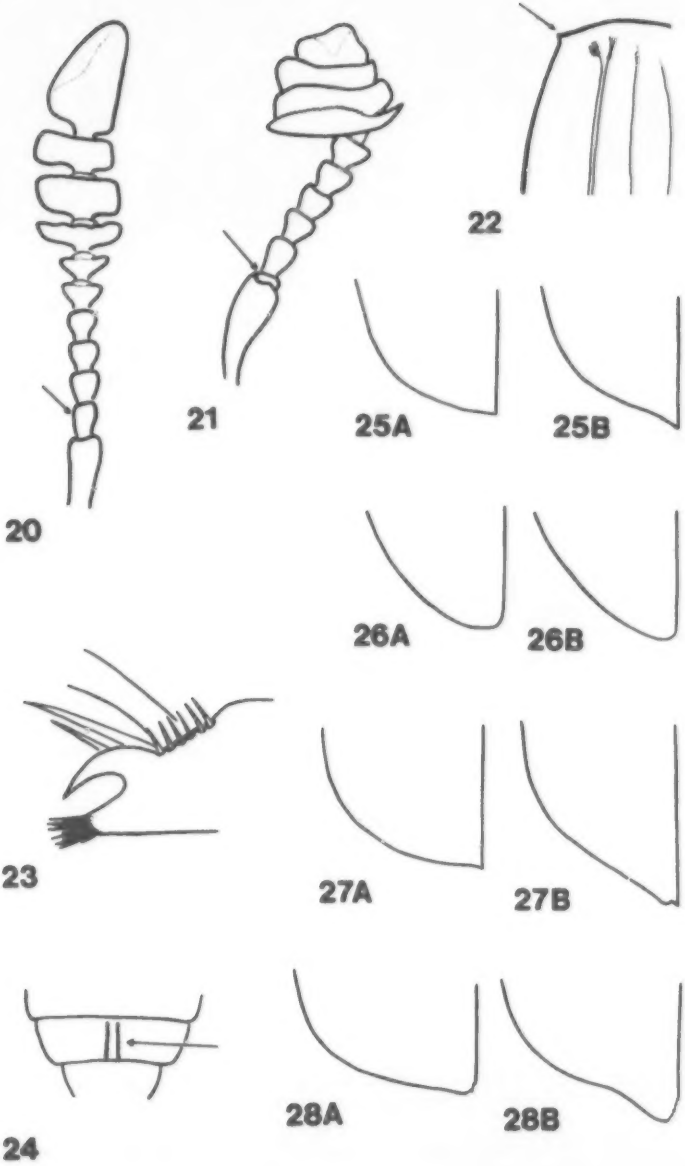

Figs. 6–11. Elytra of Silphinae (dorsal view). 6, *Thanatophilus coloradensis*; 7, *T. lapponicus*; 8, *T. trituberculatus*; 9, *T. sagax*; 10, *T. truncatus*; 11, *Necrophila americana*.




Figs. 12–14. Elytra of Silphinae (dorsal view). 12, *Necrodes surinamensis*; 13, *Oxelytrum discicolle*; 14, *Heterosilpha ramosa*.

Figs. 15, 16. Pronota of Silphinae (dorsal view). 15, *Necrodes surinamensis*; 16, *Aclypea bituberosa*.

Figs. 17–19. Pronota and postcoxal lobes of Silphinae (lateral view). 17, *Necrodes surinamensis*; 18, *Thanatophilus sagax*; 19, *T. trituberculatus*.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27A
27B
28A
28B

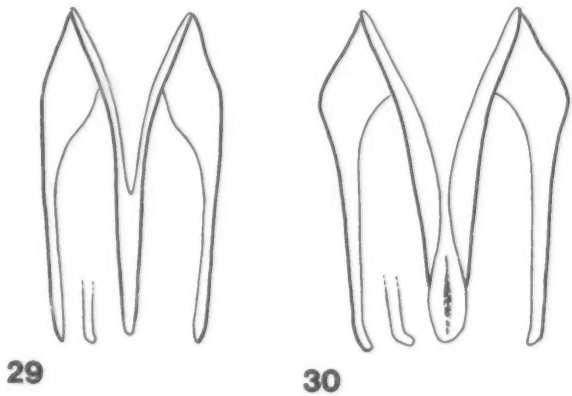
Figs. 20, 21. Antennae of adult Silphidae. 20, *Necrodes surinamensis*; 21, *Nicrophorus orbicollis*.

Fig. 22. Base of elytra of *Oiceoptoma noveboracense*.

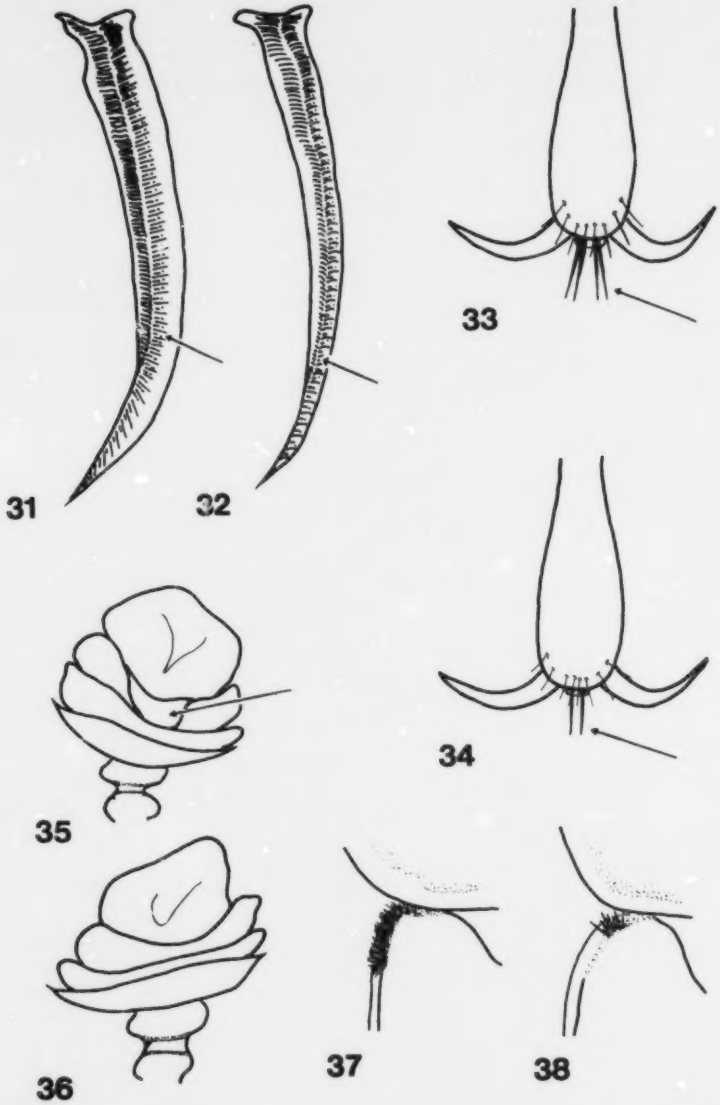
Fig. 23. Apex of metatibia of adult *Aclypea bituberosa*.

Fig. 24. Abdomen of adult *Nicrophorus defodiens*.

Figs. 25–28. Elytral apices of Silphinae (*a*, male; *b*, female). 25, *Oiceoptoma noveboracense*; 26, *Heterosilpha ramosa*; 27, *Necrophila americana*; 28, *Thanatophilus lapponicus*.




Figs. 29, 30. Apices of male genitalia of *Heterosilpha* species (dorsal view: inset shows lateral view of apex of paramere). 29, *H. aenescens*; 30, *H. ramosa*.

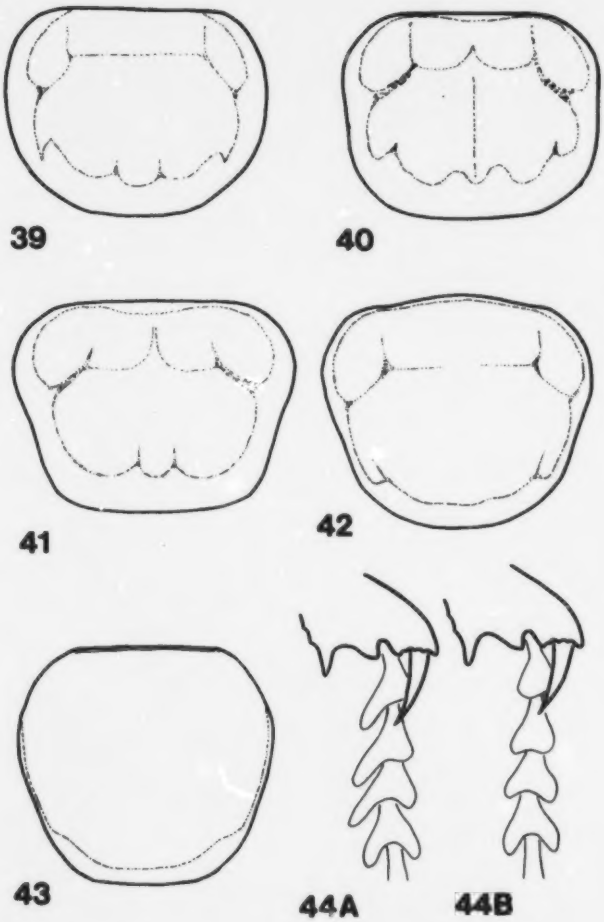



Figs. 31, 32. Elytral epipleura of *Oiceoptoma* species (ventral view). 31, *O. inaequale*; 32, *O. ruguiosum*.

Figs. 33, 34. Apical tarsal segment of adult *Nicrophorus* species. 33, *N. americanus*; 34, *N. tomentosus*.

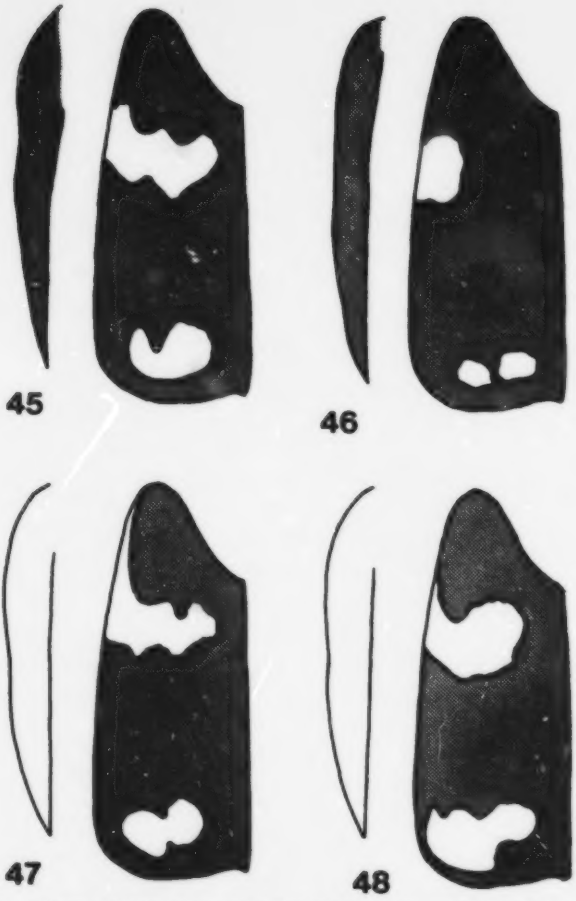
Figs. 35, 36. Antennal club of *Nicrophorus* species. 35, *N. obscurus*; 36, *N. guttula*.

Figs. 37, 38. Base of elytra of *Nicrophorus* species (dorsal view). 37, *N. hybridus*; 38, *N. investigator*.

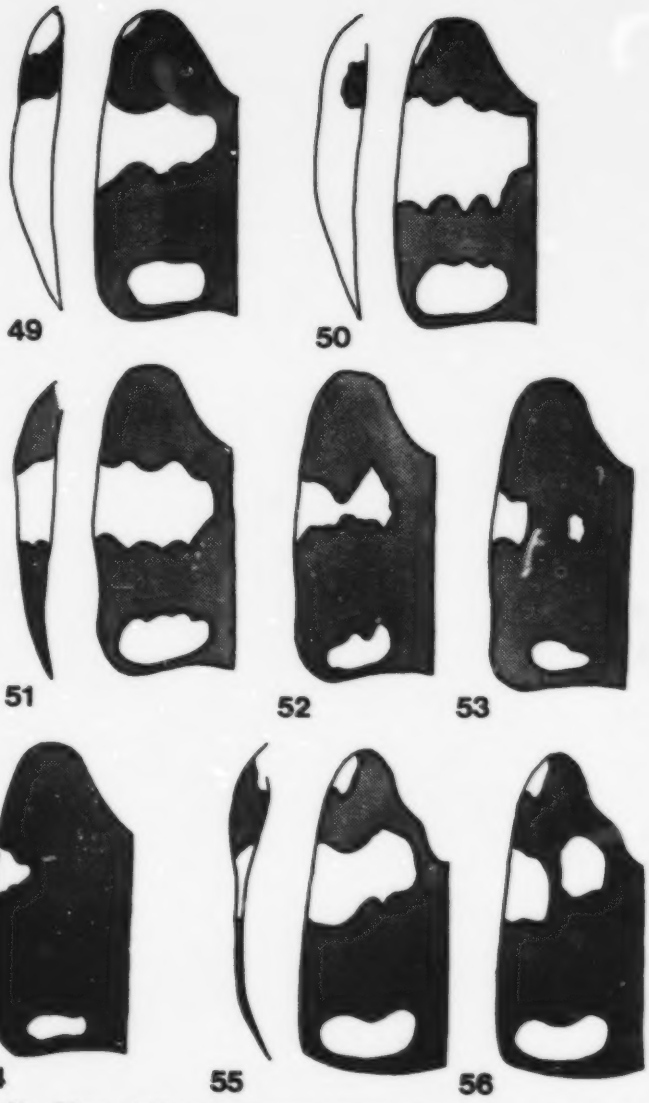



Figs. 39–43. Pronota of *Nicrophorus* species (dorsal view). 39, *N. orbicollis*; 40, *N. investigator*; 41, *N. hybridus*; 42; *N. marginatus*; 43, *N. carolinus*.

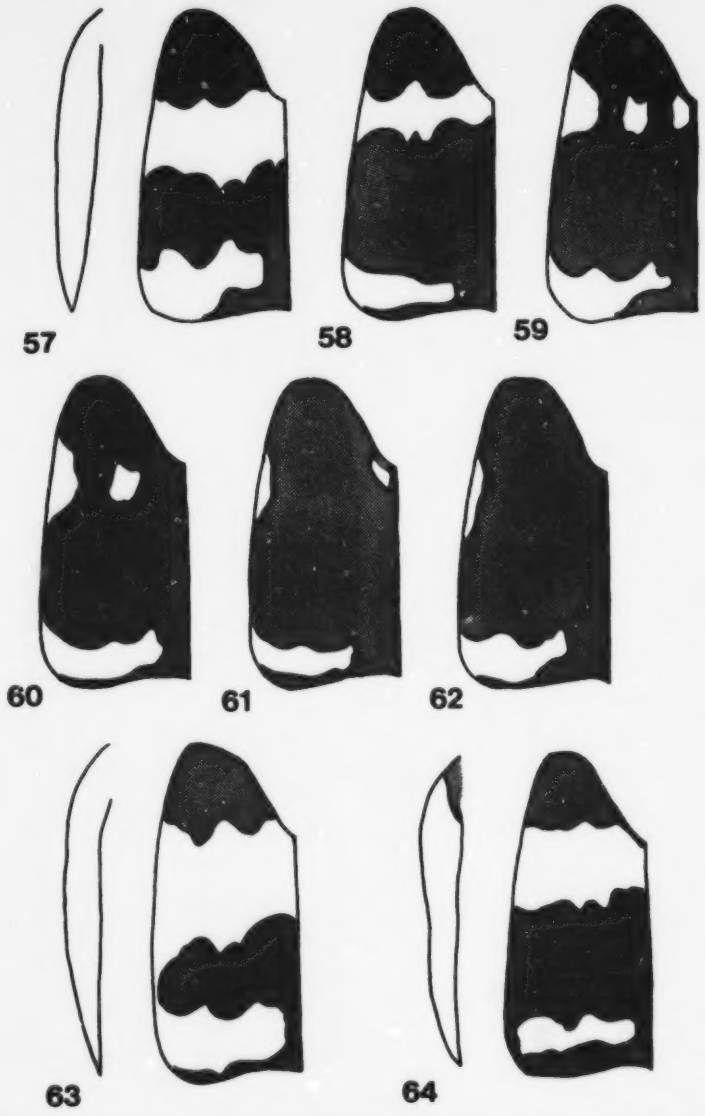
Fig. 44. Tarsi of adult *Nicrophorus orbicollis* (dorsal view: *a*, male; *b*, female).



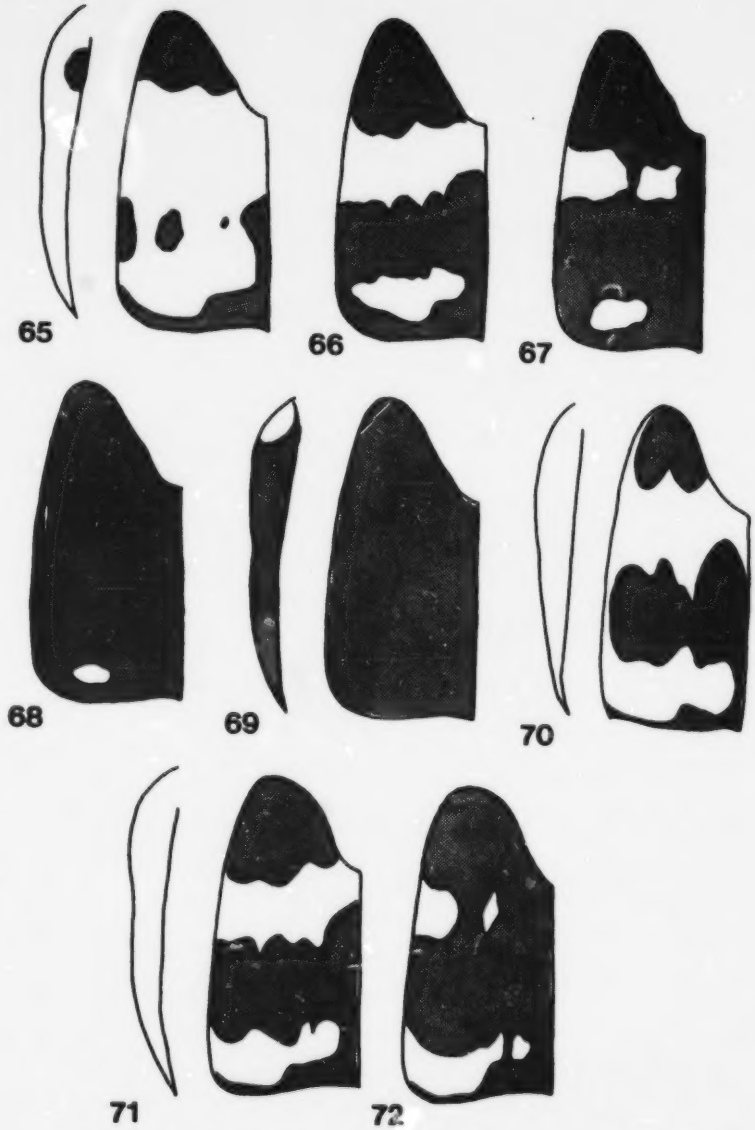

Figs. 45–48. Elytra of *Nicrophorus* species (dorsal view and lateral view of elytral epipleuron). 45, *N. orbicollis*; 46, *N. pustulatus*; 47, *N. sayi*; 48, *N. americanus*.



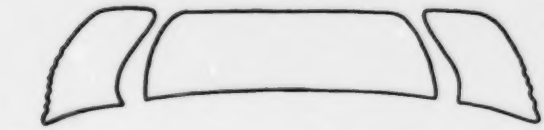

Figs. 49–56. Elytra of *Nicrophorus* species (dorsal view and lateral view of elytral epipleuron). 49, 50, *N. vespilloides*; 51–54, *N. defodiens*; 55, 56, *N. carolinus*.




Figs. 57–64. Elytra of *Nicrophorus* species (dorsal view and lateral view of elytral epipleuron). 57–62, *N. investigator*; 63, *N. hybridus*; 64, *N. tomentosus*.




Figs. 65–72. Elytra of *Nicrophorus* species (dorsal view and lateral view of elytral epipleuron). 65–69, *N. guttula*; 70, *N. marginatus*; 71, 72, *N. obscurus*.



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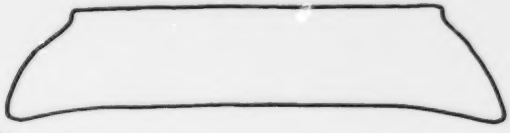

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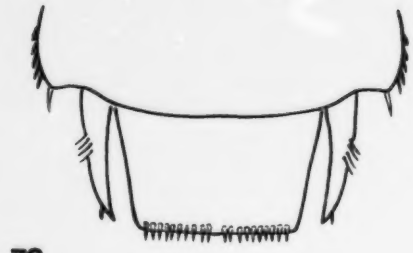
Figs. 73, 74. Sternum of second abdominal segment of larvae of Silphinae (dorsal view). 73, *Necrodes surinamensis*; 74 *Oiceoptoma noveboracense*.

Figs. 75–77. Second antennal segment of larvae of Silphinae. 75, *Oiceoptoma noveboracense*; 76, *Heterosilpha ramosa*; 77, *Aclypea bituberosa*.



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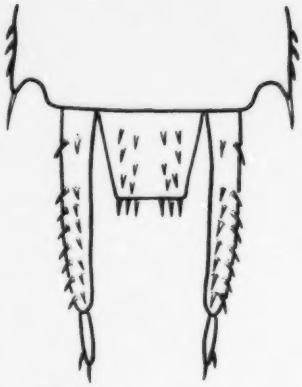

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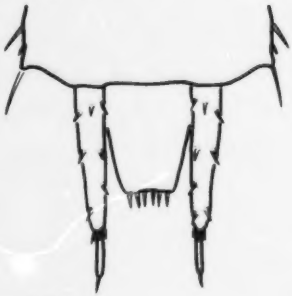

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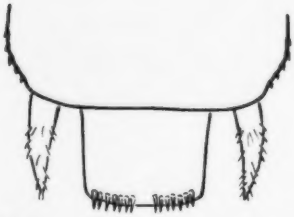

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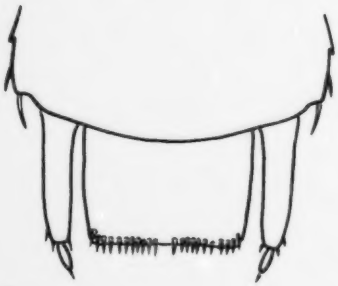

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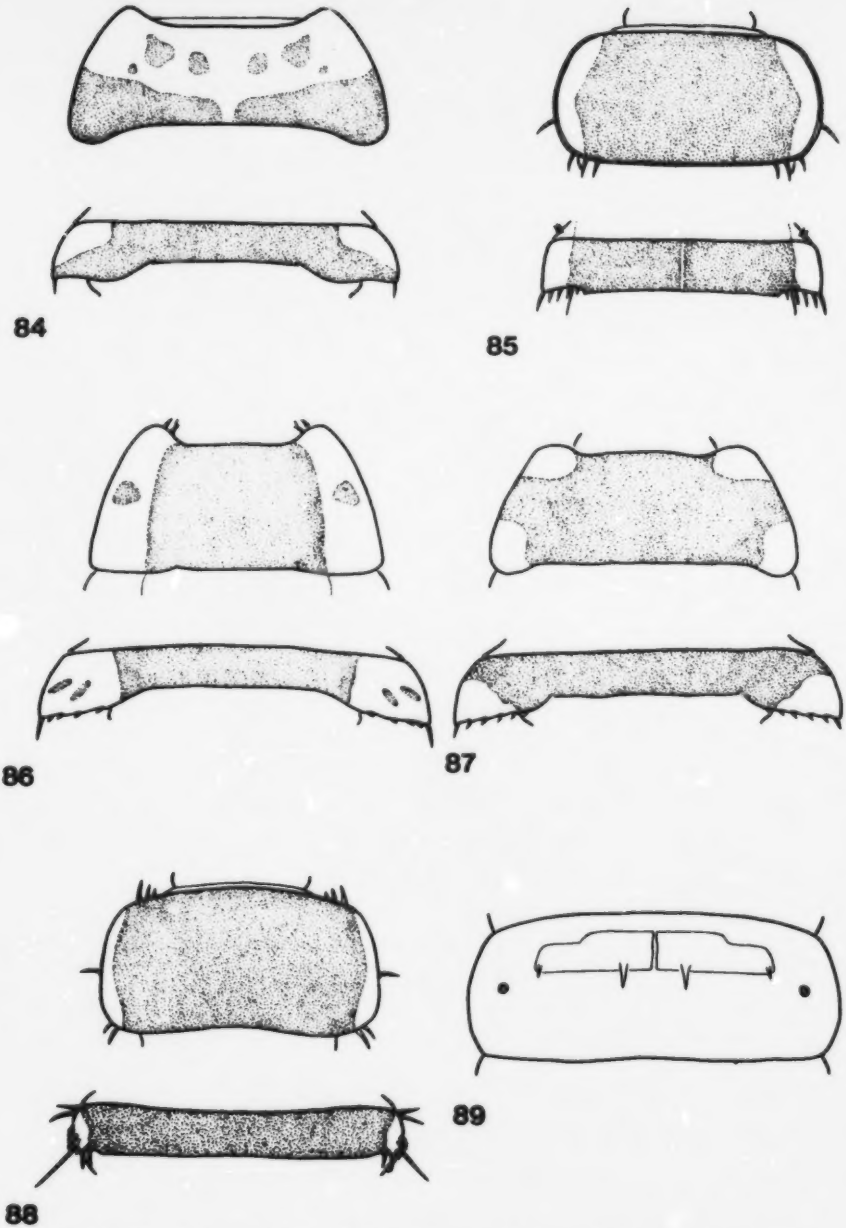
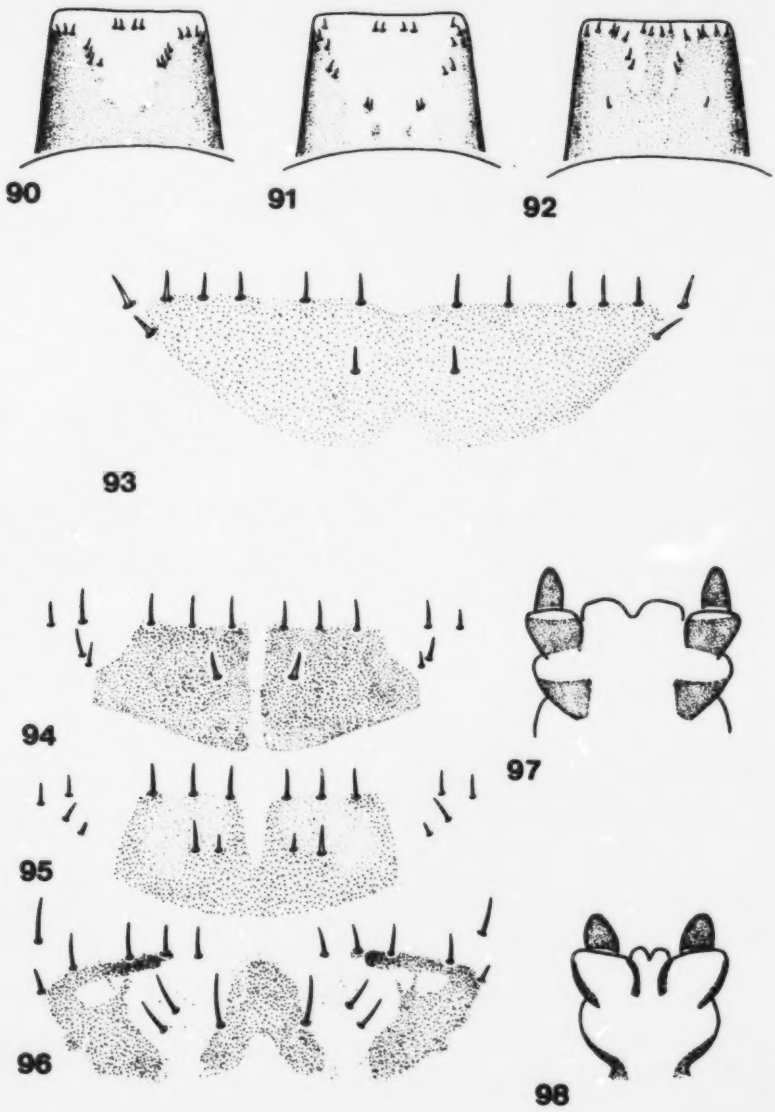
Figs. 78–83. Apex of abdomen of larvae of Silphinae (dorsal view). 78, *Heterosilpha ramosa*; 79, *Necrodes surinamensis*; 80, *Thanatophilus coloradensis*; 81, *Aclypea bituberosa*; 82, *Necrophila americana*; 83, *Oiceoptoma noveboracense*.



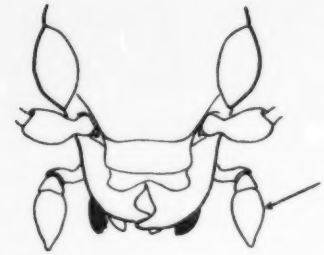

Figs. 84–89. Prothoracic and abdominal tergites of larvae of Silphidae (dorsal view). 84, *Oxelytrum discicolle*; 85, *Necrodes surinamensis*; 86, *Oiceoptoma noveboracense*; 87, *O. inaequale*; 88, *Thanatophilus coloradensis*; 89, *Nicrophorus obscurus*.




Figs. 90–92. Tenth abdominal segment of larvae of *Nicrophorus* species (ventral view). 90, *N. defodiens*; 91, *N. marginatus*; 92, *N. investigator*.

Figs. 93–96. Ninth abdominal segment of larvae of *Nicrophorus* species (ventral view). 93, *N. defodiens*; 94, *N. obscurus*; 95, *N. guttula*; 96, *N. marginatus*.

Figs. 97, 98. Labium of larvae of *Nicrophorus* species (ventral view). 97, *N. obscurus*; 98, *N. sayi*.



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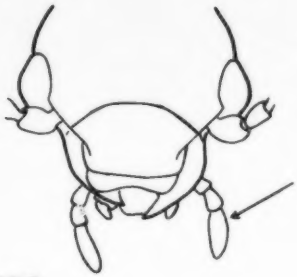

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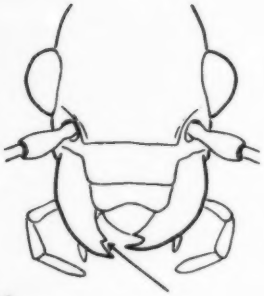

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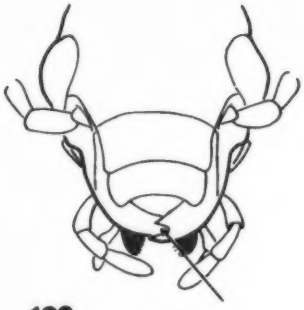

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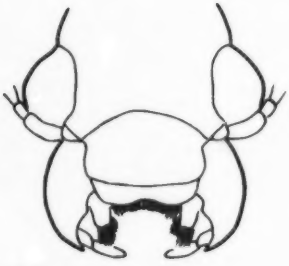

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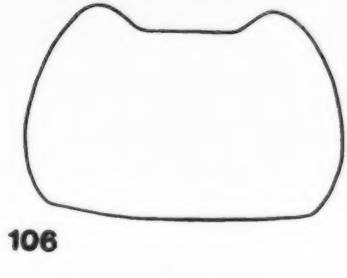
Figs. 99–103. Heads of adult Agyrtidae (dorsal view). 99, *Agyrtes longulus*; 100, *Ipelates latus*; 101, *Pteroloma nebrioides*; 102, *Apteroloma caraboides*; 103, *Necrophilus hydrophiloides*.

Figs. 104, 105. Preapical segments of antennae of adult Agyrtidae. 104, *Necrophilus hydrophiloides*; 105, *Pteroloma nebrioides*.



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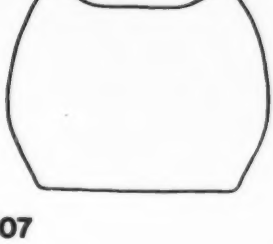

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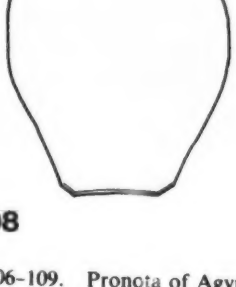

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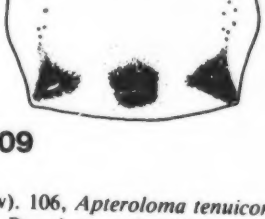

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Figs. 106–109. Pronota of Agyrtidae (dorsal view). 106, *Apteroloma tenuicorne*; 107, *A. caraboides*; 108, *Lyrosoma opacum*; 109, *Pteroloma nebrioides*.

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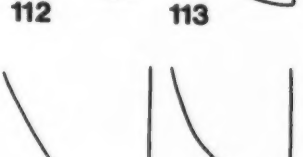

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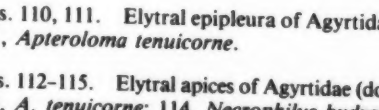

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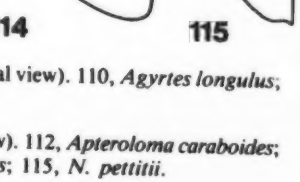

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Figs. 110, 111. Elytral epipleura of Agyrtidae (lateral view). 110, *Agyrtes longulus*; 111, *Apteroloma tenuicorne*.

Figs. 112–115. Elytral apices of Agyrtidae (dorsal view). 112, *Apteroloma caraboides*; 113, *A. tenuicorne*; 114, *Necrophilus hydrophiloides*; 115, *N. pettitii*.

# Glossary

**aedeagus** The penis, or intromittent, organ in male insects.
**allopatric** Species or populations whose distributions do not overlap.
**antenna** (pl., **antennae**) The paired segmented sensory organs borne on each side of the head.
**apical** Near or pertaining to the apex of any structure.
**aposematic** Conspicuous and warning of danger.

**basal** Near or pertaining to the base, or point of attachment to or nearest the main body of the insect.
**B.P.** Before the present. Referring to the age of fossils.

**callus** A lump, or swelling, of the cuticular surface of the insect.
**capitate** Abruptly enlarged at tip, forming a generally spherical mass.
**carina** (pl., **carinae**) Longitudinal narrow raised ridge.
**clavate** Thickened gradually toward the tip.
**clypeus** That part of the head of the insect below the front, to which the labrum is attached anteriorly.
**confluent** Running or joined together.
**contiguous** Close together or touching.
**cordate** Heart-shaped.
**costa** (pl., **costae**) Longitudinal raised ridge. Wider than carina.
**coxa** (pl., **coxae**) The basal segment of the leg.
**crepuscular** Active or flying at dusk.

**detritus** Any disintegrated or broken-down material.
**diagnosis** A short description of an insect containing only those structural characteristics that distinguish it from related forms.
**diapause** A physiological state in which development is arrested and metabolic rates are lowered.
**diurnal** Active or flying during the daylight hours.
**dorsum** The upper surface of an insect.

**ecophenotypic** Changes in structure or habits relating solely to environmental factors and not to genetic factors.
**effaced** Obliterated or indistinct.
**elytral epipleuron** See epipleuron, elytral.
**elytral interval** See interval, elytral.
**elytral shoulder** See shoulder, elytral.
**elytron** (pl., **elytra**) The hardened and leathery fore wings of beetles, which act as protective covers for the membranous flight wings.
**emarginate** With a section cut from the margin, notched.
**endemic** Distributed or found only in a given area.
**epipleural ridge** The raised upper edge of the elytral epipleuron.
**epipleuron, elytral** The folded down portion of an elytron immediately beneath the edge.
**epistomal suture** A groove separating the front of the head from the clypeus.

**eurytopic** Found in most habitats or under widely differing environmental conditions; a generalist.
**explanate** Spread out and flattened.

**family** A division of classification that may include one genus or several to many genera, all members of which are descended from a single common ancestor.
**femur** (pl., **femora**) The thigh, usually the thickest segment of the leg.
**filiform** Threadlike, slender.
**fovea** (pl., **foveae**) A deep depression, or pit.

**galea** The outer lobe of the maxilla.
**genus** (pl., **genera**) An assemblage of species agreeing in some structural feature or set of features and descended from a single common ancestor.
**glabrous** Lacking pubescence or sculpturing.

**Holarctic** Pertaining to the faunal region comprising Europe, northern Africa as far south as the Sahara, Asia south to the Himalayas, and North America south to Mexico.
**humeral angle** See shoulder, elytral.

**immaculate** Lacking a pattern of contrasting coloration.
**instar** The period, or stage, between molts in an insect larva, numbered to designate the various periods.
**insular** Referring to islands.
**interval, elytral** The space between two adjacent costae or striae.
**isodiametric** Composed of small circles of equal diameter.

**labial palpus** See palpus, labial.
**labium** The lower lip. A compound structure that forms the floor of the mouth in mandibulate insects. The fused second pair of maxillae.
**labrum** The upper lip that covers the base of the mandibles.
**lacinia** The inner lobe of the maxilla.
**ligula** The central sclerite of the labium consisting of the united left and right laciniae of the second pair of maxillae.

**maculate** Bearing a pattern of spots or markings.
**mandible** The first pair of stout and toothlike jaws in insects.
**maxilla** (pl., **maxillae**) The second pair of jaws in a mandibulate insect.
**maxillary palpus** See palpus, maxillary.
**melanism** An abnormal darkening of color pattern due to an increase in concentration of the pigment melanin.
**meso-** Prefix meaning middle.
**meta-** Prefix meaning last, or posterior.
**metasternum** The underside of the metathorax.
**metathorax** The third thoracic segment.
**metepimeron** The part of the posterior division of the metathoracic pleuron above the epimeral suture.
**midline** An imaginary line that divides the insect body into right and left halves.

**Miocene** The fourth epoch of the Tertiary period in the Cenozoic era (24 million years B.P. to 5.2 million years B.P.).
**montane** Referring to the moist cool upland slopes of mountains below timberline.
**molt** To cast off the outgrown skin or cuticle during growth.

**natural** In the sense of a group. Referring to the fact that all component members are descended from a single common ancestor.
**Nearctic** The faunal region comprised of North America, Greenland, and interior Mexico.
**necrophagous** Feeding on decaying flesh.
**Neotropical** The faunal region comprised of South America, Central America, the West Indies, and the coasts of Mexico.
**nocturnal** Active or flying during the night.
**nomenclature** The designation of a formally adopted scientific name to any biological unit.

**ocellus** (pl., **ocelli**) The eye of a larval insect, consisting of a single beadlike lens.
**orbicular** Round and flat.

**Palearctic** The faunal region comprised of Europe, Africa north of the Sahara, and Asia north of the Himalayas.
**palpus, labial** (pl., **palpi**) An elongate segmented sensory structure attached to the labium.
**palpus, maxillary** (pl., **palpi**) An elongate segmented sensory structure attached to the maxilla.
**penultimate** Next to the last.
**phoretic** Referring to the interrelationship between species of organisms in which one is carried on the body of another.
**phylogenetic** Referring to ancestor–descendant relationships or evolutionary history of a taxon.
**phytophagous** Feeding on plants or plant products.
**Pleistocene** The first epoch of the Quaternary period in the Cenozoic era (1.67 million years B.P. to 10 000 years B.P.).
**postcoxal lobe of pronotum** The lateral projection behind the coxa of the first pair of legs.
**pro-** Prefix meaning first, or anterior.
**pronotum** The upper shieldlike surface of the prothorax.
**pubescence** Short, fine, closely set hairs.

**quadrate** Composed of four equal sides. Square.

**reticulate** Composed of a network of fine lines.
**rugose** Wrinkled.

**sclerite** A hardened, usually darkly colored piece of the insect body bounded by sutures.
**sculpture** Pattern of impressions or elevations on a surface.

**sensillum** (pl., **sensilla**) A simple sense organ.
**sensu latu** In the widest or largest sense.
**sensu stricto** In the narrowest sense.
**shoulder, elytral** The outer basal angle of the elytron, also known as the humeral angle.
**species** A reproductively isolated group of interbreeding populations.
**spiracle** A breathing pore in insects located laterally on certain body segments.
**sternite** A sclerotized component of the sternum.
**sternum** The underside of a particular thoracic or abdominal segment.
**stria** (pl., **striae**) A fine longitudinal impressed line.
**stridulate** To make a hissing, grating, or creaking noise by the rubbing together of two roughened surfaces.
**subquadrate** Composed of four unequal sides.
**subspecies** A geographically isolated population whose members are characterized by one or more structural differences, and are capable of interbreeding should they be brought into contact with one another.
**symbiosis** The living together of two or more species of organisms in an intimate association.
**sympatric** Species or populations whose distributions overlap at least in part.
**synonym** One of two, or more, different names for the same taxon.

**tarsus** (pl., **tarsi**) The apical segment of the insect leg bearing the claws.
**teneral** Lightly colored, soft, newly emerged stage of an insect.
**tergite** A sclerotized component of the tergum.
**tergum** The upper surface of a particular thoracic or abdominal segment.
**thanatosis** The act of faking death.
**tibia** (pl., **tibiae**) The fourth division of the insect leg.
**trochanter** The small segment of the insect leg between the coxa and the femur.
**transverse** Wider than long.
**truncate** Cut off squarely at the tip.

**unnatural** Referring to a taxon whose component members are not all descended from a single common ancestor.
**urogomphus** (pl., **urogomphi**) Fixed or mobile processes found on the terminal segments of some insect larvae.

**venter** The undersurface of an insect.

**Wisconsinan** The most recent subdivision of the Pleistocene in North America, characterized by extensive continental glaciation.

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